Larval Life in the Leaves: Arboreal Tadpole Types, with Special Attention to the Morphology, Ecology, and Behavior of the Oophagous *Osteopilus brunneus* (Hylidae) Larva

Abstract

Osteopilus brunneus tadpoles were collected from bromeliads in Jamaica. Among the unusual morphological features of these larvae are greatly reduced gill filters and gill filaments, enlarged muscles for depressing the jaws and buccal floor, and an elongate tail with reduced tail fins. Most of the unique morphological features of *O. brunneus* tadpoles can be accounted for by the evolution of early metamorphic onset in an otherwise generalized hylid larva. The normal tadpole resting posture is vertical, with the head pointing upward. Larvae are obligate air-breathers and can survive for more than a day on a wet surface, out of water. When submerged, they do not pump water through their buccopharyngeal cavity, but only open their mouths to take in air and food. We suggest that gill filament and tail fin reduction serve to reduce O_2 loss to the hypoxic water of bromeliads. Based on the breeding behavior of the adults and the association of tadpoles with frog eggs, we conclude that *O. brunneus* larvae are obligatorily oophagous, on unfertilized conspecific eggs. We review what is known about other aboreal tadpoles and conclude that *O. brunneus* represents one of at least five distinct arboreal larval types. These types correlate with tadpole diet and microhabitat differences in the arboreal environment. Based on Inger's (1958) definition of a genus, *O. brunneus* and *O. septentrionalis* are probably not congeners.

Introduction

> ... one of the Brown Frogs begins his song of kuk-kuk, kuk-kuk, which another takes up, and another, and another, until his friends around him have joined in the strains ... very soon the sound increases and advances, for the thing is catching, and thousands and thousands of little throats in near-by woods join in the hubbub, until from hill to hill it passes coming on and on but always dying away in the rear as it proceeds, then after reaching and passing up, the sound of this pulsating wave of harmony—for indeed it is harmony—becomes less and less, and fainter and fainter. . . .

> Panton, describing
> an *Osteopilus brunneus* chorus,
> quoted in Dunn (1926).

Orton (1953), in a now-classic paper, discussed and illustrated the adaptive radiation of anuran tadpoles. In her figure seven and in the text, the arboreal tadpole type is described simply as a "thin, flattened larva." While this is a common morphology for arboreal tadpoles, it is now known that arboreal tadpoles assume a variety of shapes and sizes. Tadpoles of the genera *Theloderma, Anotheca,* and certain *Hyla* live in arboreal habitats, but do not fit the Orton type (Duellman, 1970; Wassersug et al., 1981).

Two questions emerge: What is the range of variation in tadpole morphology within the arboreal habitat, and how does this morphological variation relate to microhabitat and behavioral differences?

In this paper we examine aspects of the chondrocranial morphology, cranial myology, internal oral anatomy, lateral line system, and overall growth of the arboreal bromeliad-dwelling tadpole of the Jamaican hylid *Osteopilus brunneus* and compare it to a currently recognized congener, *O.*

septentrionalis (Trueb & Tyler, 1974), which has a generalized pond larva. Additionally, we examine several aspects of the behavior and ecology of *O. brunneus* tadpoles, including swimming performance, aerial respiratory patterns, anoxic tolerance, and tolerance to subaerial exposure. In the field we examined the natural associations of adults, tadpoles, and eggs and give evidence for the production of trophic eggs. We also survey most of the literature on the morphology and behavioral ecology of arboreal tadpoles in other families and genera and define five arboreal types. Finally, following the ideas of Inger (1958) on the concept of the genus, based on the great difference in the morphology and way of life of *O. brunneus* and *O. septentrionalis,* we conclude that these two species are not valid congeners.

Literature Review

Trueb and Tyler (1974) reviewed the taxonomic history of *Osteopilus brunneus* and assigned the species to its current position based on gross adult morphology. Dunn (1926) described bromeliad dwelling and oophagy in Jamaican hylids, including *O. brunneus,* and illustrated the elongate tadpole morphology and external oral features, emphasizing in simple line drawings the reduction of keratinized mouthparts in these larvae. External oral features of Jamaican hylids were also illustrated in Noble (1931). Orton (1944), in an unpublished doctoral dissertation, described some aspects of the external morphology, jaw musculature, jaw cartilages, and skeleton in *O. brunneus* and several other arboreal hylid larvae. She concluded that the arboreal type of tadpole has been converged upon in several anuran families. More observations on the tadpole morphology and behavior of Jamaican hylids, including relative gill filament size, aerial respiration, and swimming, can be found in another unpublished doctoral thesis by Jones (1967). His major focus, however, was on trying to understand why certain frogs, including *O. brunneus,* concentrate the green pigment bilevirdin in their bones. Laessle (1961) described and quantified several physicochemical properties of tadpole-bearing bromeliads, including their temperature and dissolved oxygen (DO) concentrations, and speculated on the behavior of *O. brunneus* tadpoles (see below). Noble (1927), in his classic study of anuran life histories, mentioned *O. brunneus* and discussed its larval biology in the context of anuran phylogeny. Noble (1929) later

examined the morphological adaptations of certain African arboreal tadpoles and used *O. brunneus* as an outgroup for comparison. Shreckenberg (1956) described thyroid gland development in *O. brunneus* and in doing so provided general developmental data.

Methods

We studied *Osteopilus brunneus* both in the field in Jamaica and in our laboratory.

Field Observations

Fieldwork was done during September 1984 and May 1985 on the grounds of the Hollywell Recreation Centre (Jamaican Forest Department) located in Hardwar Gap at the western end of the Blue Mountains of Jamaica at 1250 m elevation. The Hollywell Centre consists of 3 to 5 ha of partly cleared parkland surrounded by montane mist forest (Asprey & Robbins, 1953). Epiphytic bromeliads are common, both in the forest and on trees in the parkland, and occur in clusters of up to 10 plants. Bromeliads were identified using Adams (1972), and identifications were confirmed at the herbarium of the University of the West Indies in Mona, Jamaica.

We found *O. brunneus* by localizing calling males to bromeliad clusters at night. On a subsequent day, all the bromeliads in a cluster were carefully taken down and dissected and all *O. brunneus* eggs, tadpoles, and adults collected. We also arbitrarily chose and sampled some clusters from which we had not heard males calling. Most eggs and tadpoles were preserved in 10% neutral buffered formalin within two hours of collection. Developmental series of nine clutches were obtained by sampling, at regular intervals, eggs maintained in our cabin at 20 to 25°C. Adults were measured (snout-vent length, SVL) and sexed by their size (females average 15 to 20 mm longer than males; Schwartz & Fowler, 1973; Trueb & Tyler, 1974), association with spontaneously shed eggs, or calling behavior (which males continued even after capture). About 60 live tadpoles were brought back to Dalhousie University, where we studied several aspects of their physiology and behavior.

Laboratory Observations

In the laboratory we examined and staged (according to Gosner, 1960) a sample of 75 preserved *O. brunneus* eggs and 140 tadpoles. Tadpoles were measured (SVL and total length; tail length, TL, was obtained by subtraction), and their guts examined for food. Twenty larvae at different stages were dissected to examine their stomach contents.

We described the external morphology and internal oral and gross gastrointestinal anatomy of *O. brunneus* tadpoles using both light and scanning electron microscopy. Specimens were prepared for the electron microscope by the technique used by Wassersug and Rosenberg (1979) and Wassersug and Duellman (1984). Specimens of *O. septentrionalis* from Florida, first described by Duellman and Schwartz (1958), were similarly examined for comparison with *O. brunneus*.

In the laboratory we observed the normal behavior of 60 *O. brunneus* tadpoles. We also examined their (1) swimming kinematics, (2) aerial respiratory responses to variations in DO level, (3) aquatic anoxic tolerance, and (4) resistance to subaerial conditions. Because of the difficulty of transporting live tadpoles from Jamaica to Canada and the need to use tadpoles of the same developmental stages in our tests, sample sizes for some of our behavioral studies were small.

Where variance measures are given in the text, they are in the form of standard error about the mean.

SWIMMING—We examined the swimming performance of 10 *O. brunneus* tadpoles using high-speed cinematographic techniques. Tadpoles ranged from 14 to 28 mm total length (stages 25 to 28) and swam in still water at 21 ± 1°C. Films were taken with a Locam (Red Lake Corp., Campbell, Calif.) high-speed motion picture camera at 250 f/s with a 50-mm macro lens. The camera was located about 60 cm above the floor of a 50- × 50- × 20-cm aquarium. Two 650-watt incandescent lamps about 40 cm from the aquarium provided illumination. Thirteen swimming bouts were analyzed and examined with a Hewlett Packard image analysis system consisting of an HP9834A minicomputer and an HP9872A digitizer.

We recorded variations in the following: tail beat frequencies (f); length of the propulsive wave (λ); maximum amplitude at the tail tip (A); specific amplitude at varying distances along the body; and one measure of mechanical efficiency, Froude efficiency (η). All kinematic measures were made over as large a range of swimming speeds (U, in body lengths per second, Ls^{-1}) as possible according to the method of Wassersug and Hoff (1985). Only sequences of constant or nearly constant (± 0.3 U) velocity were used in these analyses.

AERIAL RESPIRATORY PATTERNS—Six *O. brunneus* tadpoles (stages 25 to 41, SVL 5 to 14 mm) were exposed to each of five levels of DO from 1.5 to 12.2 mg/liter. The DO levels were varied by bubbling N_2 through aged, previously aerated tap water for various lengths of time; longer N_2 bubbling resulted in lower DO levels. For each trial N_2 was bubbled into 1.5 liters of water, 200 ml of which was poured with minimum agitation into each of six 500-ml Erlenmeyer flasks, to a depth of between 35 and 40 mm; temperature was 21.0°C. One tadpole was carefully added to each flask, then each flask was capped with a rubber stopper. Tadpoles were acclimated for 20 minutes, then we counted numbers of times they surfaced to breathe air during a 30-minute period. The DO levels were measured before each trial using a modified Winkler field kit (Model 8931; Ecologic Instrument Corp., Long Island, N.Y.). This method is accurate to within 0.2 mg/liter. Treatments were presented in a staggered fashion; viz., in the order 3.2, 12.2, 1.5, 10.5, and 7.5 mg/liter. Tadpoles were rested and allowed to feed for at least four hours between treatments.

ANOXIC TOLERANCE—We compared 12 *O. brunneus* tadpoles with equal numbers of *Xenopus laevis* and *Rana sylvatica* tadpoles. We attempted to use tadpoles of as similar developmental stage, SVL, and wet weight as possible. *Osteopilus* were in stages 25 to 31, SVLs ranged from 5.0 to 10.8 mm, and wet weights ranged from 0.2 to 0.4 g. *Xenopus* and *Rana* were laboratory stock that had been maintained for several weeks in aerated water and were growing normally. *Xenopus* tadpoles were in stages 27 to 31, had SVLs from 10.0 to 14.6 mm, and weighed 1.3 to 1.5 g. *Rana* tadpoles were in stages 25 to 27, had SVLs from 8.5 to 9.3 mm, and weighed 0.5 to 0.6 g.

Twelve tadpoles of each species were divided into two groups of six larvae per species and placed in separate glass staining dishes (75 × 95 × 60 mm deep) filled with aged, previously aerated tap water at 21.5°C. The six dishes were then covered with nylon mesh (8 meshes/cm) secured by rubber bands and divided into two groups of three, each containing tadpoles from one of the species. Both groups were then submerged in separate larger tanks filled to a depth of 90 mm with aged tap water. This arrangement deprived the larvae access to the water's surface to gulp air. Aquatic DO con-

FIG. 1. **A,** One large and two small clusters of the bromeliad *Hohenbergia fawcettii* on a tree at the Hollywell Recreation Centre study site. The large cluster is about 4 m above the ground. **B,** A single *H. fawcettii* plant in seed. Note serrations along leaf margins.

centrations in both tanks at the beginning of this experiment were 12.2 mg/liter. Three air lines connected to air stones were placed in one tank, and the water was aerated to maintain a high DO level. Initially, the second tank was not aerated, and its DO level was allowed to decrease naturally as a result of tadpole respiration. After 93 hours the DO in the unaerated tank was 3.4 mg/liter, the DO in the aerated tank was 10.5 mg/liter, and all tadpoles were alive. At that point we became concerned that starvation might become a factor in our results. To reduce this chance and shorten the experiment, we induced severe hypoxic conditions by bubbling N_2 through air stones in the previously unaerated tank. During the next four hours of this treatment, the DO level gradually decreased to 1.6 mg/liter. We observed and recorded tadpole activity and viability at regular intervals until all of the *Rana* and *Xenopus* larvae were dead.

RESISTANCE TO SUBAERIAL CONDITIONS—To examine the relative resistance of *O. brunneus* to being out of water, we compared 12 tadpoles (four *O. brunneus,* four *X. laevis,* and four *R. sylvatica*) in subaerial conditions and observed their survival and behavior. We attempted to standardize developmental stage, SVLs, and wet weights among species, which in part accounts for the small sample sizes. The *O. brunneus* tadpoles in this experiment ranged from stages 37 to 40, had SVLs of 10.5 to 14.0 mm, and weighed 0.4 to 0.9 g. Laboratory stock *Xenopus* and *Rana* were again used for comparison. *Xenopus* tadpoles ranged from stage 31 to 34, had SVLs from 12.5 to 14.2 mm, and weighed 1.2 to 1.4 g. *Rana* tadpoles ranged from stage 27 to 29, had SVLs from 22.0 to 23.5 mm, and weighed 1.8 to 2.4 g.

We placed individual tadpoles on separate pieces of filter paper cut to fit into 50-mm diameter Petri dishes. The paper was wetted with 2 ml of aged tap water and the dishes were covered. Observations began at 0900 on day 1 and were terminated at 0730 of day 3 after all tadpoles died. Tadpoles were initially observed every 15 minutes and then every 30 minutes, but were not observed between

2400 and 0730 of days 2 and 3. If there was doubt about whether a tadpole was still alive, it was gently prodded to induce movement.

Results and Discussion

Ecology and Behavior

We sampled 23 clusters of epiphytic bromeliads containing one to 10 plants each ($\bar{x} = 4.3 \pm 0.6$ plants per cluster) and located 1 to 7 m above the ground. Fourteen of these clusters were composed of *Hohenbergia fawcettii* ($\bar{x} = 5.3 \pm 0.8$ plants per cluster, range 1–10) a large bromeliad with thick, stiff, spiny-marginate leaves (fig. 1). Seven clusters were composed solely of *Guzmannia fawcettii* ($\bar{x} = 1.8 \pm 0.5$ plants, range 1–3), a large bromeliad with flexible, nonspiny leaves. The two remaining clusters contained a mixed assemblage of *H. fawcettii* and *Vriesia sintenisii,* a moderate-sized, smooth-leaved bromeliad.

Osteopilus brunneus was found exclusively in *H. fawcettii*; we heard males call only from clusters of that species. Of the 23 clusters that we sampled, frogs, larvae, or eggs were collected from 11 pure *H. fawcettii* clusters and one mixed cluster ($\bar{x} = 5.8 \pm 0.8$ plants per cluster, n = 12, range 2–10). *Osteopilus brunneus* was never associated with *G. fawcettii*. This biased association of *O. brunneus* may involve some aspect of *H. fawcettii* that is advantageous to the frogs, such as the spiny leaf margins or more vertical leaf orientation yielding a deeper and darker central tank, or may simply reflect a preference for larger bromeliad clusters. Indeed, at Hardwar Gap, *H. fawcettii* and *G. fawcettii* are the predominant large bromeliad species, but only the former consistently forms large aggregated clusters. A preference for *H. fawcettii,* however, cannot hold throughout Jamaica since this plant only occurs at moderately high elevations in the Blue Mountains (Adams, 1972), a small portion of the geographic range of *O. brunneus* (Schwartz & Fowler, 1973). We have heard *O. brunneus* calling at elevations up to 1650 m on the flanks of Blue Mountain Peak, where *H. fawcettii* does not occur, but were unable to locate the bromeliads which held the calling frogs.

Eggs and Larvae—Twenty-six bromeliads in 11 clusters contained eggs and/or tadpoles of *O. brunneus,* including 13 plants with just eggs, seven plants with eggs and tadpoles, and six plants containing tadpoles alone. Tadpoles and eggs were

Table 1. A summary of the sexes, sizes (SVL in mm) and associations of adult *Osteopilus brunneus* collected at Hardwar Gap.

| Adult | Sex | SVL | Associations | |
			In same plant	In same cluster
A	M	48.5		t
B	M	51.5		B + C, e, t
C	M	47.5		
D	M	50.5	e, t	e
E	F	55.5		e, t
F	M	44.5		
G	F	59.0	e	
H	M	46.0	H + I	G–J, e, t
I	M	45.5		
J	F	59.5	e, t	
K	M	49.0	K + L	
L	F	61.5		K–M, e, t
M	Escaped			

Each adult is identified on the left by a capital letter and brackets to the right; e = associated eggs, t = associated tadpoles.

usually found in the central tanks of bromeliads. Tadpoles, even those in late developmental stages, were always associated with the gelatinous remnants of egg capsules, which made the water in these tanks highly viscous.

In September 1984 we found no eggs. At that time tadpoles were present in five bromeliads of the three clusters we sampled. These tadpoles ranged from stages 25 to 44 and occurred in groups of six to 25 per bromeliad. We also collected three recently metamorphosed froglets (SVL 20 to 25 mm) from one cluster.

In May 1985, in contrast, tadpoles collected from eight plants ranged from stages 21 to 31 and, with one exception, co-occurred with eggs. Tadpole numbers at that time ranged from three to 36 per bromeliad. We obtained accurate counts of the numbers of eggs in 18 of 20 bromeliads, which yielded an average of 276 ± 44 eggs per bromeliad (range 20–622). The majority of eggs were developing normally and ranged from stages 3 to 20. Hatching in *O. brunneus* occurs early, at about stage 21. Tadpoles are oophagous after stage 24 (see below); however, the number of eggs in bromeliads with tadpoles present ($\bar{x} = 312 \pm 100$, n = 6, range 20–597) was not significantly different from that with tadpoles absent ($\bar{x} = 258 \pm 46$, n = 12, range 79–662; $P > 0.2$), suggesting that developing eggs are not being eaten by tadpoles.

Adults—We captured a total of 12 adult *O. brunneus* from seven bromeliad clusters ($\bar{x} = 7.0 \pm$
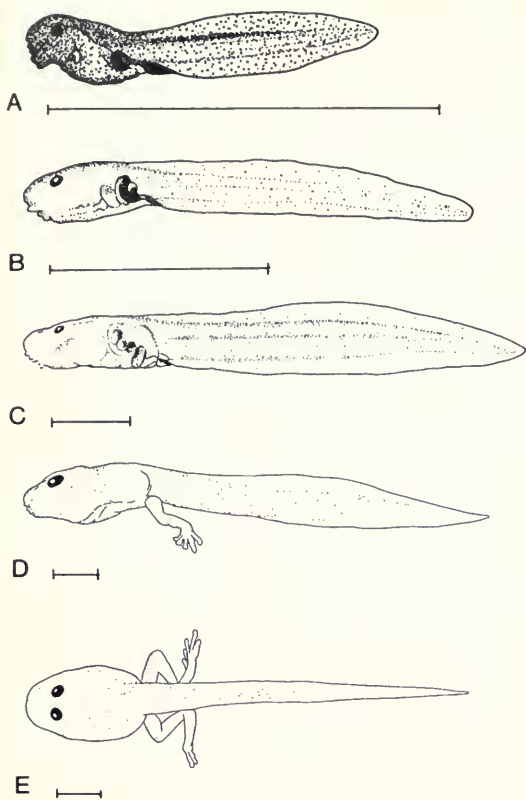
FIG. 2. Illustration of a premetamorphic developmental series of *Osteopilus brunneus* larvae. Developmental stages according to Gosner (1960). **A**, Stage 21; **B**, stage 25; **C**, stage 30; **D-E**, stage 41. All scale lines = 5 mm.

2.8 plants per cluster, range 2–10). Four adults were found alone in individual clusters, the other eight occurred in aggregations of two to four frogs per cluster (table 1). The largest aggregation, four adults, included a pair of males (H, I) that occupied a large bromeliad, and two females (G, J), each of which occupied separate plants. Another cluster, containing two males (B, C) in separate plants, was the only cluster from which we ever heard more than one male call. A third cluster contained three adults, including a male-female pair (K, L; not in amplexus) in one bromeliad and a third adult (M) that escaped from another plant during collection.

Associations of adults with eggs and tadpoles are given in Table 1. Eggs and/or tadpoles occurred in six of the seven clusters that contained adults. Five clusters that contained eggs and/or tadpoles, but no adults, were significantly smaller than those with adults present ($\bar{x} = 4.2 \pm 1.0$ plants per cluster, range 2–8 vs. $\bar{x} = 7.8 \pm 1.9$ plants per cluster,

range 5–10; t test, $P < 0.05$). Hence, eggs may be deposited in smaller clusters than adults normally inhabit. However, the numbers of clutches (counting eggs and tadpoles as separate clutches) in clusters that contained adults ($\bar{x} = 4.3 \pm 2.2$, n = 6, range 2–8) was significantly greater than clusters without adults ($\bar{x} = 1.4$, n = 5, range 1–2; $P < 0.05$), indicating that more clutches are deposited in the larger clusters—the ones that the frogs normally inhabit—than in the smaller ones.

There is no clear pattern in the association of adults and offspring in individual bromeliads. Of 10 adults that we could assign to particular bromeliads, three frogs, a male (D) and two females (G and J), occurred in plants with eggs and/or tadpoles. The male-female pair (K, L) was in a bromeliad that contained neither eggs nor tadpoles. After capture, the pair were put together in a reconstructed bromeliad and left undisturbed for 36 hours. They did not assume amplexus and no eggs were laid. Three of the four females spontaneously shed eggs in collecting bags from one to several days after capture. Two of them did so twice in the space of two weeks following capture. We maintained the eggs, but none of them developed.

Calling behavior differed markedly between September 1984 and May 1985. In May calling was intensive, with nightly choruses that occurred in intermittent bouts that seemed to pulse (Dunn, 1926; see introductory quote). Bouts of chorusing lasted approximately 30 seconds to two minutes and occurred once or twice per hour. At Hardwar Gap, a single male generally called from each cluster, with the exception of the two males that called from one cluster (noted above). In September calling was sporadic, usually by single males or neighboring pairs; choruses never developed.

Differences between May and September in calling behavior and the presence of developing eggs suggest a distinct seasonality to reproduction by *O. brunneus* at Hardwar Gap, corroborating the observations of Dunn (1926) and Jones (1967).

INTERACTIONS AMONG LIFE HISTORY STAGES: TADPOLE DIETS, OOPHAGY, AND PARENTAL CARE— The stomachs of stage 21 to 24 tadpoles contained detritus, similar to the allochthonous material found in the bottoms of bromeliad tanks. It is unusual for tadpoles to feed before stage 25, when the opercular flap closes over the external gills. We do not know whether this detritus is actively or passively ingested.

The stomachs of stage 25 to 41 tadpoles contained predominantly whole frog eggs, specifically
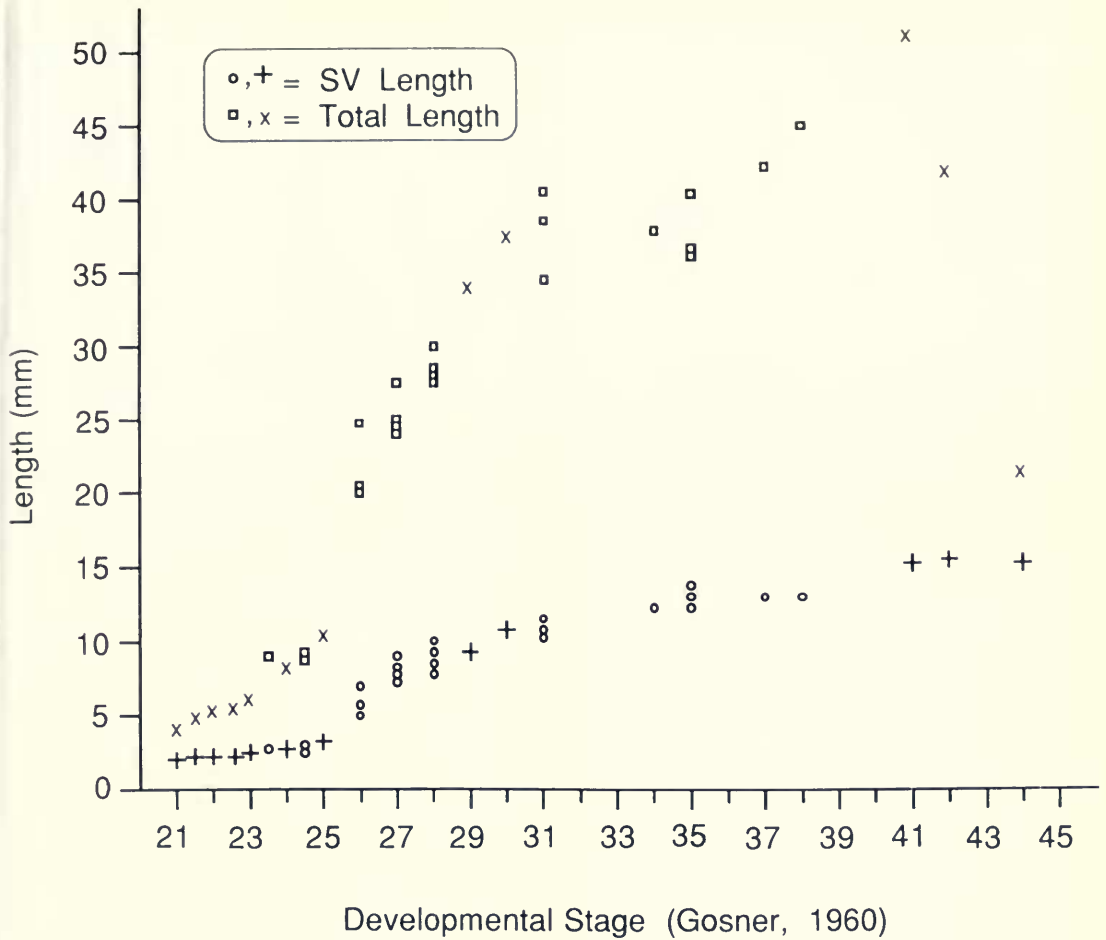
FIG. 3. Growth data for *Osteopilus brunneus* larvae. Circles and squares indicate individual specimens, crosses and X's indicate means for samples of five or more specimens at the same developmental stage. Total length increases faster than snout-vent (SV) length between stages 25 and 30, indicating that much of the growth of these tadpoles during earlier larval development is because of a disproportionate increase in tail length.

O. brunneus eggs since no other anurans with aquatic eggs occur in the Hardwar Gap area. Of 47 tadpoles that we examined, 37 had only eggs in their stomachs; the other 10 contained only detritus. The average number of eggs in 10 stomachs was 35 ± 16.0 (range 5–184). There appeared to be a positive relationship between number of eggs and the size and stage of tadpoles. For example, a stage 27 (SVL 7 mm) tadpole had 12 eggs in its stomach and one intact egg in its intestine, a stage 37 (SVL 13 mm) tadpole had 25 eggs in its stomach and none in its intestine, whereas a stage 41 (SVL 15 mm) tadpole had 184 eggs in its stomach and two in its intestine. The larger number of eggs found in these stomachs compared with the few intestinal eggs suggests that eggs pass into the intestine a few at a time. Eggs in stomachs

never appeared digested, while those in intestines were usually highly digested, suggesting that the stomach is predominantly a storage site and that most, if not all, digestion takes place in the intestine.

Ingested eggs from tadpoles collected in both September and May always appeared undeveloped ($<$ stage 3). They were granular, usually light colored, and closely resembled eggs that were spontaneously shed by adult females in our collecting bags. We never found evidence of tadpoles eating other tadpoles.

Arboreal tadpoles of several tropical frogs are known to eat eggs (Dunn, 1926, 1937; Taylor, 1954; Jones, 1967; Duellman, 1970; Wassersug et al., 1981; Weygoldt, 1987; this study). In *Dendrobates pumilio* (Weygoldt, 1980), *D. histrionicus* (Zim-

FIG. 4. Scanning electron micrograph of the oral region in an *Osteopilus brunneus* larva. Note the deficiency in the oral disk dorsally. Reduced denticle rows and oral disk characterize macrophagous arboreal tadpoles. Scale line = 1.0 mm.

mermann & Zimmermann, 1981), and *D. speciosus* (Jungfer, 1985) females lay unfertilized eggs specifically as food for their arboreal tadpoles. Our observations of *O. brunneus,* along with those of Jones (1967), suggest that trophic egg production may occur in this species as well. Four lines of evidence support this view: (1) seasonality of fertilized egg production, (2) aseasonality of trophic egg production, (3) tadpole stomach morphology, and (4) increasing numbers of ingested eggs with tadpole size.

First, as we noted above, we found developing eggs and young larvae in bromeliads during May 1985, but only larvae during September. These observations suggest that breeding does not occur in September. This conclusion is corroborated by Jones (1967) and our own observations on calling. Second, most larvae collected in both May and September had stomachs that contained undeveloped eggs. This suggests that unfertilized eggs are deposited during the latter part of tadpole development, past the time when adults are breeding. Third, stomach morphology indicates that this organ acts as a storage site, suggesting a morphological response to an abundant but discontinuous food source. Fourth, because larger, older larvae had more eggs in their stomachs than younger larvae, these stomachs must be periodically refilled. None of this would be possible if tadpoles were only eating fertilized eggs and breeding took place during a brief period in the spring. Furthermore, we found larvae and eggs together in bromeliads during May. The majority of eggs were developing normally and ranged from stages 3 to 19, yet the eggs contained in tadpole stomachs showed no signs of development. Hence, it does not appear that tadpoles are continuously feeding on younger, prehatching tank-mates. We also collected spontaneously shed nonfertile eggs in our collecting bags, indicating that females have the physiological ability to periodically provision tadpoles.

Larval Growth and Development

A developmental series for *O. brunneus* is illustrated in Figure 2. Growth data (fig. 3) indicate that total length increases much faster than SVL from stages 25 to 30. Tail elongation occurs after
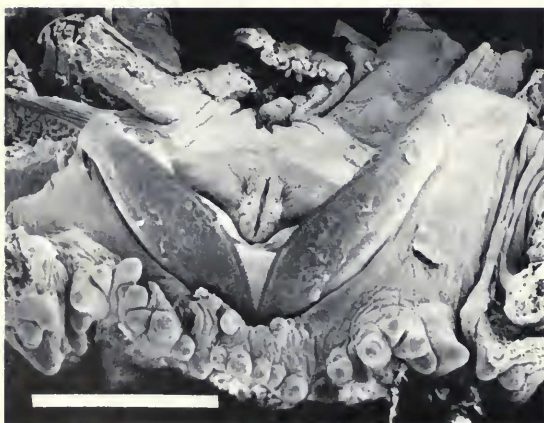

FIG. 5. Scanning electron micrograph comparison of the lower beak in *Osteopilus brunneus* (**left**) and *O. septentrionalis* (**right**) larvae. Note the V-shaped lower beak in *O. brunneus* in anterior view. *Osteopilus septentrionalis* have three lower denticle rows that are absent in *O. brunneus*. The large, patent glottis of *O. brunneus* may be readily seen between the two sides of the beak. The same region in *O. septentrionalis* is obscured from view by infralabial papillae. Scale line = 1.0 mm.
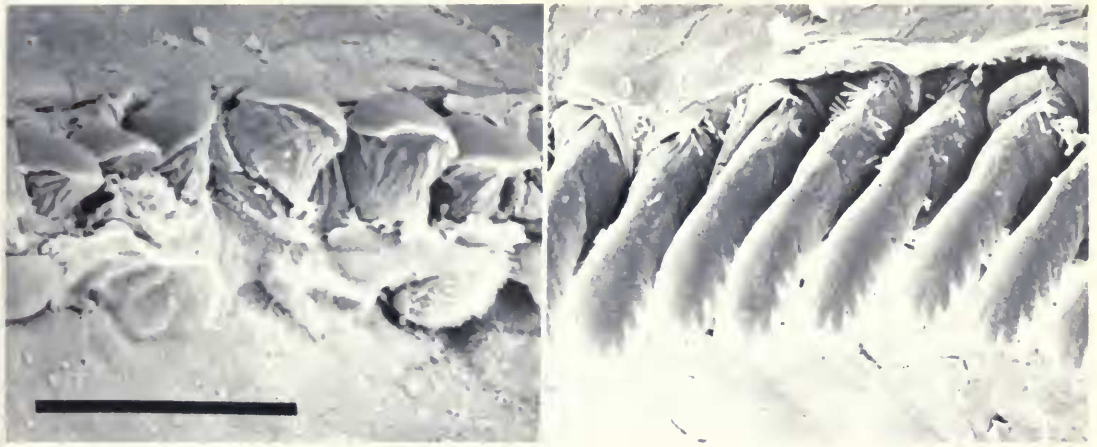
FIG. 6. Scanning electron micrograph comparison of denticles from upper denticle rows of *Osteopilus brunneus* (**left**) and *O. septentrionalis* (**right**) larvae. Note the short blunt denticles in *O. brunneus*. Scale line = 0.05 mm.

hatching. This change in gross body proportions seems unusual for tadpoles which usually grow isometrically; for example, the posthatching elongation seen in *O. brunneus* does not occur in pond-dwelling *Bufo valliceps* (Limbaugh & Volpe, 1957) and *Rana capito* larvae (Volpe, 1957).

We cannot convert Gosner stages to larval age for field-collected animals because we could not maintain natural food and temperature regimes for hatchlings raised in our laboratory. In our most complete laboratory series, eggs developed from stages 17 and 18 to stage 21 (hatching) in 72 hours, and from stage 21 to 25 in 170 hours.

Larval Morphology

The following description is based on six *Osteopilus brunneus* tadpoles. One individual each was used to describe: (1) external morphology, (2) internal anatomy and myology, (3) internal oral surface features, (4) chondrocranium and buccal pump morphology, and (5) lateral line topography. All individuals were in stage 37, except the specimen used to describe lateral line topography, which was in stage 25.

EXTERNAL FEATURES—An elongate, ventrally flattened tadpole, SVL 11.1 mm; total length 41.2 mm; body widest behind eyes, 6.0 mm; width at eyes 5.9 mm; maximum depth of body 4.3 mm; eyes directed more dorsally and laterally than anteriorly; minimum distance between eyes 2.0 mm, maximum outside diameter of eyes 4.0 mm.

In dorsal view there is a long extension of the snout past the nares, snout shovel-like; nostrils average size, directed anterolaterally; internarial distance = interocular distance.

Lateral and ventral skin transparent; spiracle sinistral, patent, located on edge of flattened ventral surface slightly more than halfway back on the body, no elevated flap present on spiracle; anus relatively long tube extending onto ventral fin, opening at or close to midline; lateral line neuromasts not conspicuous.

Tail long and thin, 38 myotomes in tail, 46 overall, myotomes extending forward to back of eye; no tail fin on body proper; terminal portion of tail slightly rounded; myotomes near tail tip widely separated by myosepta; maximum height of tail (5.0 mm) occurs 58% caudal to tip of snout; tail at highest point = 60% muscle, 25% dorsal fin, 15% ventral fin; fin height does not decrease as rapidly posteriorly as muscle does, so that dorsal and ventral fins are subequal in size and equal in height to muscle in last 10% of tail.

Mouth ventral, wide (width 2.4 mm); upper and lower beaks present (fig. 4), lower beak strongly notched with opposing sides at 90° (fig. 5); tiny serrations on both beaks; one upper denticle row with 72 very fine, blunt denticles lacking marginal cusps (fig. 6); no lower denticle rows; no distinct oral disc but blunt, marginal papillae surrounding mouth except for dorsal one-third over upper beak, papillae large, more globose laterally.

CHONDROCRANIAL AND BUCCAL PUMP MORPHOLOGY—The chondrocranium of *O. brunneus* is similar to that of other macrophagous tadpoles in that the rostral region is broad and the palatoquadrate bars are robust. The chondrocranium overall is depressed; the processus muscularis is shallow, as in *Anotheca spinosa* (see fig. 3 in Wassersug & Hoff, 1982). The ceratohyals are oriented at 45° to the long axis of the tadpole rather than
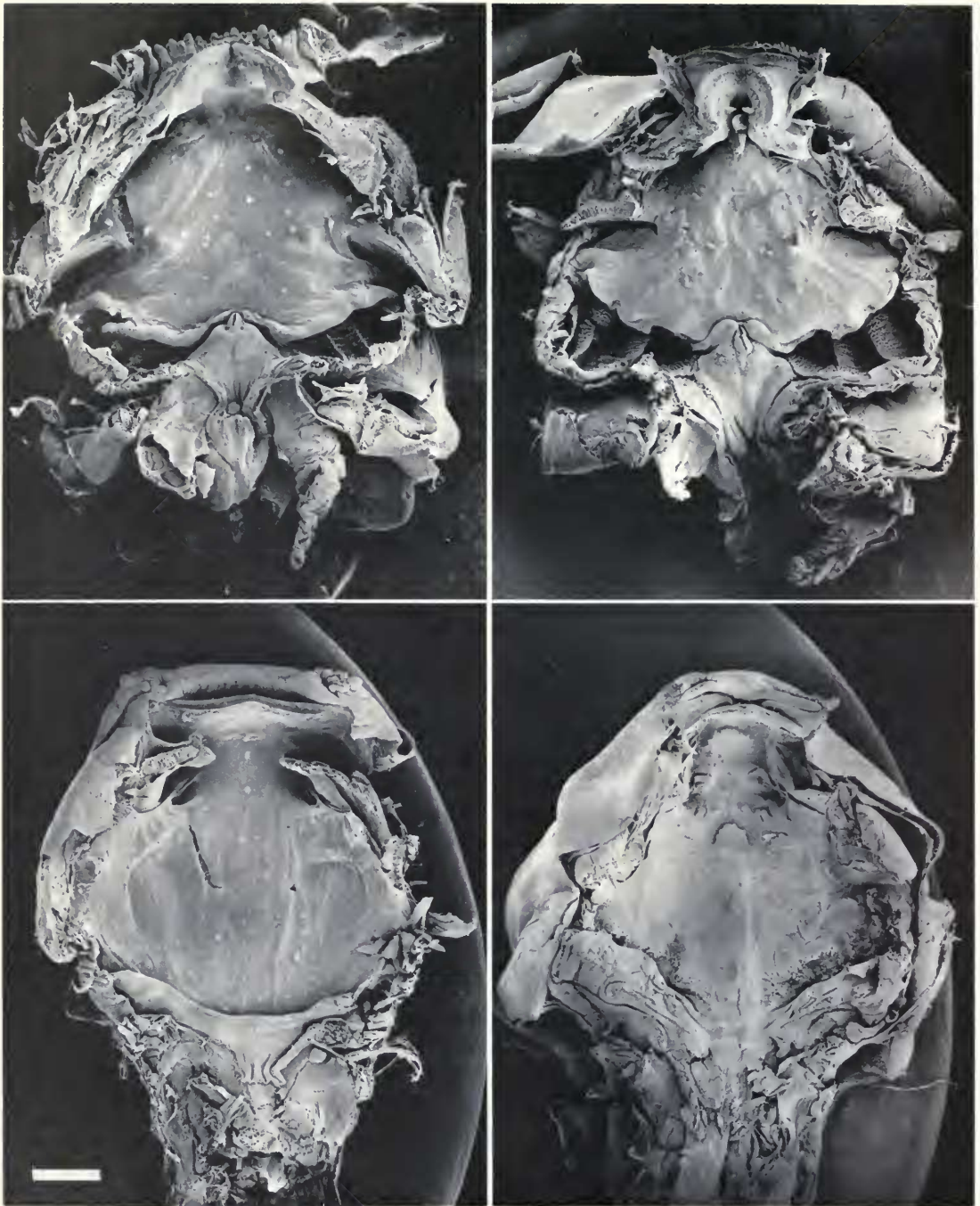
Fig. 7. Scanning electron micrograph of floor (top) and roof (bottom) of *Osteopilus brunneus* (left) and *O. septentrionalis* (right). Note the lung buds to the left and right sides of the esophagus (top SEMs; left bud partially removed) in both specimens. Scale line = 1.0 mm.

transversely. The lateral lever arm of the ceratohyal is long; lever arm ratio (Wassersug & Hoff, 1979) equals 0.37. This is high for tadpoles in general (x̄ for 40 species = 0.32) but average to

low for obligate macrophagous larvae (e.g., ratio 0.40 for *A. spinosa*). The ceratohyals are short along the rostrocaudal axis, but a large buccal floor area is nevertheless achieved because of a very large

hypobranchial plate. The branchial baskets are small and shallow.

Using equations from the work of Wassersug and Hoff (1979), we calculate a buccal volume of 5.1 μl for an *O. brunneus* tadpole (SVL 12.7 mm). This is more than twice that predicted for a typical, generalized pond larva of comparable size (table 6 and fig. 8 in Wassersug & Hoff, 1979). Assuming 90% contraction of the orbitohyoideus muscle during buccal floor depression, the ceratohyal of *O. brunneus* rotates through 27° with each buccal pump stroke, which is typical for tadpoles in general ($\bar{x}$ for 40 species = 26°).

BUCCOPHARYNGEAL SURFACE FEATURES (FIGURE 7)—**Ventral Features**—Mouth broad anteriorly; all buccal papillae (e.g., infralabial, lingual, buccal floor arena papillae, etc.) absent (fig. 8); about 20 distinct pustules scattered about buccal floor; glottis large, patent, anteriorly directed (fig. 5), fully exposed between broad medium notch of ventral velum; marginal papillae on ventral velum absent (fig. 9); secretory cells on free edge of ventral velum opening individually between squamous epithelial cells rather than into large pits; branchial baskets small and shallow; gill filters with tertiary filter folds of low density (fig. 10); gill filter rows number 4, 5, 7, and 7 for ceratobranchials 1 through 4, respectively; filter plates extremely shallow, unimbricated; filter rows few; gill slits visible in dorsal view; isolated secretory cells in branchial food traps, but secretory ridges absent (fig. 11); gill filaments absent; large esophagus.

Dorsal Features—Prenarial region very broad and smooth, lacking surface projections (fig. 12); nares transversely oriented; narial valves simple, without prenarial papillae or narial valve projections; median ridge absent; all other papillae commonly found on the buccal roof of tadpoles absent, but about 20 pustules scattered about roof; secretory zone indistinct; no enlarged or elevated secretory pits; dorsal velum with smooth anterior edge continuous across midline (fig. 13); a single weakly defined pressure cushion visible on each side; ciliary groove shallow but cilia present.

MYOLOGY AND ABDOMINAL ANATOMY—The most conspicuous muscle seen through the ventral skin is the very large orbitohyoideus; angularis complex and interhyoideus muscles are also large. The ratio of cross-sectional areas for the muscles that operate the ceratohyal pump, the interhyoideus and orbitohyoideus, is 0.39, which is low compared with that of *Anotheca spinosa* (0.55) but much higher than the average ratio for other macrophagous larvae (cf. Satel & Wassersug, 1981).

FIG. 8. Scanning electron micrograph of the front of the buccal floor of an *Osteopilus brunneus* larva (**top**) and an *O. septentrionalis* larva (**bottom**). Note that the beak is wider and more anteriorly directed in *O. brunneus* than in *O. septentrionalis*. Note also the absence of infralabial and buccal floor papillae in *O. brunneus*. Scale line = 1.0 mm.

[Not included here are *Hyla bromeliacia* and *H. dendroscarta*, which were erroneously considered macrophagous by Satel and Wassersug (1981), who followed Salthe and Mecham (1974) in this error.] The myotomal musculature extends to back of eye.
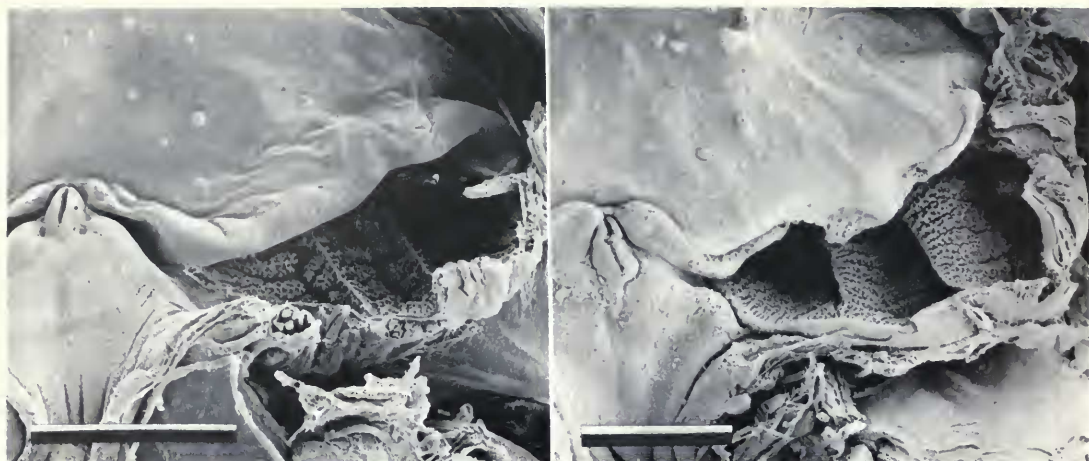
FIG. 9. Scanning electron micrograph of right branchial basket in dorsal view of an *Osteopilus brunneus* larva (**left**) and an *O. septentrionalis* larva (**right**). Note the thickened, papillate-free edge of the ventral velum in *O. brunneus*. Note also ciliary fields in the esophagus of both species. Scale line = 1.0 mm.

Liver visible through ventral skin, massive, filling about one-fourth of body cavity, three-lobed; gut tube not double-coiled as in most tadpoles; stomach sacculate; maximum diameter of empty stomach 2.1 mm, diameter increases greatly when stomach contains eggs; stomach runs obliquely across whole abdominal cavity, J-shaped, with shorter ascending arm on right side; small intestine 0.4 to 0.6 mm in diameter; majority of intestinal coils lie in lower left quadrant of body cavity but additional short switch-back coils in lower right quadrant, i.e., many places where intestine folds back on itself, but tight, multiply coiled pattern

FIG. 10. Scanning electron micrograph close-up of medial half of right branchial basket of an *Osteopilus brunneus* larva. Note the shallow nature of the filter plates and low density of the filter mesh. Compare with SEM of *O. septentrionalis* in Figure 9. Scale line = 0.5 mm.
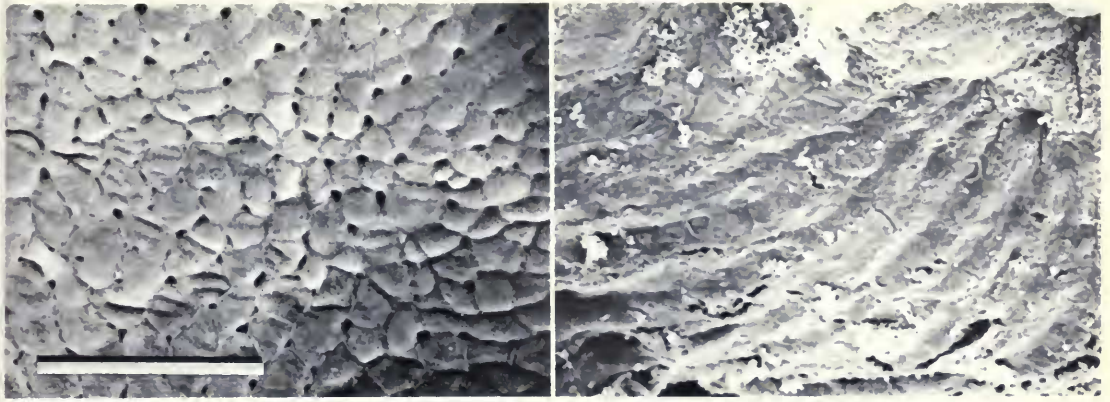
absent; expanded ampullae at junction of large and small bowel; large intestine oriented obliquely from left and rostral to right and caudal across lower abdomen, visible through skin in ventral view; gut length from esophagus to anus 75.5 mm; gut length to SVL ratio 6.3.

Lungs small, about one-half body length. Fat bodies in abdomen large, with six, finger-like projections.

LATERAL LINE TOPOGRAPHY—Neuromasts singular, not forming stitches (fig. 14); a total of 18 supra- and infraorbital neuromasts per side.

Comparison of *Osteopilus septentrionalis* with *O. brunneus*

Duellman and Schwartz (1958) describe the external morphology of the *O. septentrionalis* tadpole. Here we augment their description for purposes of comparison with *O. brunneus*. We dissected two animals. The first was at stage 37, with SVL 14.5 mm and total length 31.5 mm, which was much larger than stage 37 *O. brunneus* tadpoles. The second animal was equal to or slightly smaller than our dissected *O. brunneus* larvae; it was stage 29, with SVL 10.3 mm and total length 27.1 mm.

The *O. septentrionalis* tadpole is a typical pollywog in most characteristics including overall body shape and intestinal organization. Lateral line neuromasts are conspicuous. With minor exceptions, the internal oral morphology of *O. septentrionalis*

FIG. 11.   Scanning electron micrograph close-up of secretory surfaces from the branchial food traps of *Osteopilus brunneus* (**left**) and *O. septentrionalis* (**right**) larvae. Note that isolated secretory pits are present in *O. brunneus*, but they are not organized into either rows or ridges as in *O. septentrionalis*. Scale line = 0.05 mm.

is virtually identical to that of generalized hylid larvae described by Wassersug (1976, 1980). Thus, only a very abbreviated description is given here.

CHONDROCRANIAL AND BUCCAL PUMP MORPHOLOGY — The chondrocranium is that of a generalized hylid larva. The buccal pump morphology of this species was considered by Wassersug and Hoff (1979) in their comparative study of the tadpole buccal pump mechanism. The processus muscularis is of average dimensions; the ceratohyals are oriented transversely. The lever arm ratio for the arms of the ceratohyal is 0.29. The buccal volume for a tadpole of 15.5-mm SVL given in Wassersug and Hoff (1979) is 7.4 μl, which is high for a tadpole of this size, but much less than that of *O. brunneus*.

BUCCOPHARYNGEAL SURFACE FEATURES (FIGURE 7) — **Ventral Features** — Two pairs of infralabial papillae, a small, more dorsal pair and a larger, more ventral pair that cross at the midline and partially obstruct the oral orifice (figs. 7–8); two small lingual papillae; buccal floor area large; buccal floor arena (BFA) broad, bounded by 10 to 12 BFA papillae per side; medial notch of the ventral velum very large, with the neighboring papillae of the ventral velum folded forward (fig. 9); free velar margin with large secretory pits; branchial baskets large and deep; gill filter density high; numbers of gill filter rows are 9, 12, 16, 10 for ceratobranchials 1 through 4, respectively; branchial food traps with distinct secretory ridges (fig. 11; ridges not well preserved in this specimen); glottis large, patent, dorsally directed.

Dorsal Features — Anteriorly directed, archlike

ridge in prenarial area; anterior edge of narial valves pustulate; narial valve with large pustulate narial valve projection; three postnarial papillae on each side running in oblique rows from anteromedial to posterolateral; a few other pustulations scattered in postnarial arena; median ridge of average size with semicircular free anteroventral edge; lateral ridge papillae small, about half the size of the median ridge, with irregularly sculptured margins; other buccal roof papillae absent; dorsal velum with smooth free edge, broadly divided on the midline; two large, ill-defined pressure cushions per side; ciliary groove distinct.

MYOLOGY AND ABDOMINAL ANATOMY — Neither the orbitohyoideus nor the angularis musculature of these tadpoles is exceptionally large. The liver is smaller than in *O. brunneus*. Gut length for a stage 37 animal was 128 mm; gut length to SVL ratio, 9.2. Fat bodies with fewer finger-like projections than in *O. brunneus*.

While it is well established that herbivorous tadpoles on the average have longer alimentary canals than related carnivorous species (Noble, 1931), it is difficult to compare the relative gut lengths for tadpoles given in different studies. The gut length to SVL ratio of 6.3 that we obtained for *O. brunneus* is similar to or higher than values reported for more generalized, nonobligatory macrophagous tadpoles in previous studies (e.g., $\bar{x}$ = 5.3, range 1–11 in Heyer, 1973; $\bar{x}$ = 3.6, range 1.4–8.1 in Altig & Kelly, 1974; $\bar{x}$ = 4, range 3–5 in Wilczynska, 1981). However, such measurements are particularly prone to artifact (Heyer, 1973). Using great care we obtained a gut length to SVL ratio
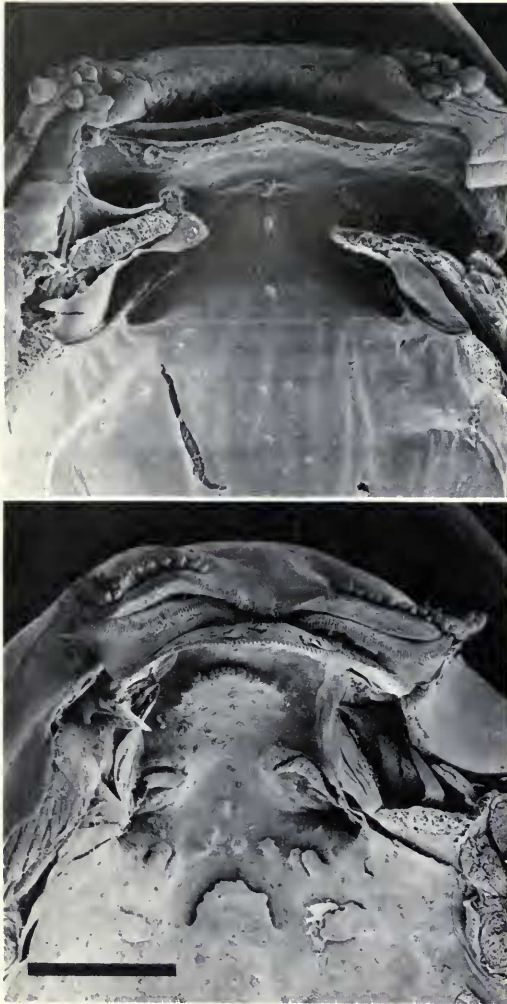
FIG. 12. Scanning electron micrograph of the front of the buccal roofs of an *Osteopilus brunneus* larva (**top**) and an *O. septentrionalis* larva (**bottom**). Note that the mouth is broader in *O. brunneus* and that all prenarial and postnarial surface projections seen in *O. septentrionalis* are absent in *O. brunneus*. Scale line = 1.0 mm.

of 9.2 for *O. septentrionalis*, but we do not believe that the gut is exceptionally long in this tadpole. Of greater significance is the relative difference between species; the gut of *O. brunneus* is 32% shorter than that of comparatively sized *O. septentrionalis*.

LATERAL LINE TOPOGRAPHY — Neuromasts form stitches, on average two neuromasts per stitch were present (fig. 14); 69 supra- and infraorbital stitches were present, yielding a total of about 138 neuromasts per side, which is approximately seven to eight times more neuromasts than *O. brunneus* has at the same developmental stage.

Overall Comparison and the Evolution of the *Osteopilus brunneus* Larva

The internal morphological features that most readily distinguish *O. brunneus* from *O. septentrionalis* and other generalized hylid larvae are as follows: (1) a wider buccal floor and mouth, (2) reduced buccal floor and roof papillae, (3) enlarged anteriorly directed glottis, (4) smaller and shallower branchial baskets with half as many gill filter rows, (5) reduced gill filaments, (6) no secretory ridges in the branchial food traps, (7) undivided dorsal velum, (8) enlarged orbitohyoideus and angularis musculature, (9) enlarged liver, and (10) sacculate stomach. In addition the lateral line neuromasts are greatly reduced.

Certain features, surprisingly, do not differ between the two forms. For example, larvae of both species have moderate, but not exceptional, lung development and a fully exposed glottis on the buccal floor. This latter feature suggests that aerial respiration is important for *O. septentrionalis*, as well as for *O. brunneus*. Both species have relatively large buccal pump volumes for tadpoles of their size, *O. brunneus* more so than *O. septentrionalis*.

The vast majority of features that distinguish *O. brunneus* from *O. septentrionalis* larvae are features associated with metamorphic morphology in pond larvae. At metamorphosis in typical tadpoles: denticle rows are lost; the gill filaments and gill filters are reduced; the glottis enlarges and becomes fully exposed on the buccal floor; buccal
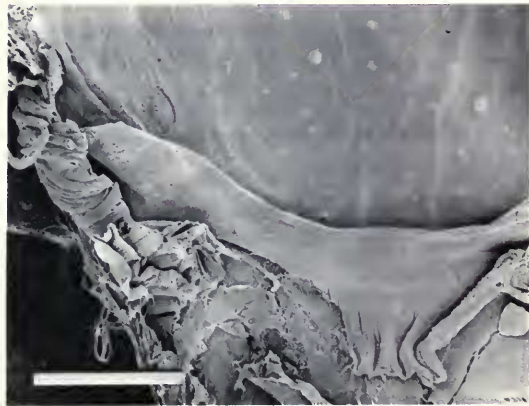

FIG. 13. Scanning electron micrograph of the posterior right corner of the buccal roof of an *Osteopilus brunneus* larva in ventral view. Note that the dorsal velum is completely continuous across the midline. A pressure cushion on the velum is barely present; the ciliary groove, however, is distinct. Scale line = 1.0 mm.
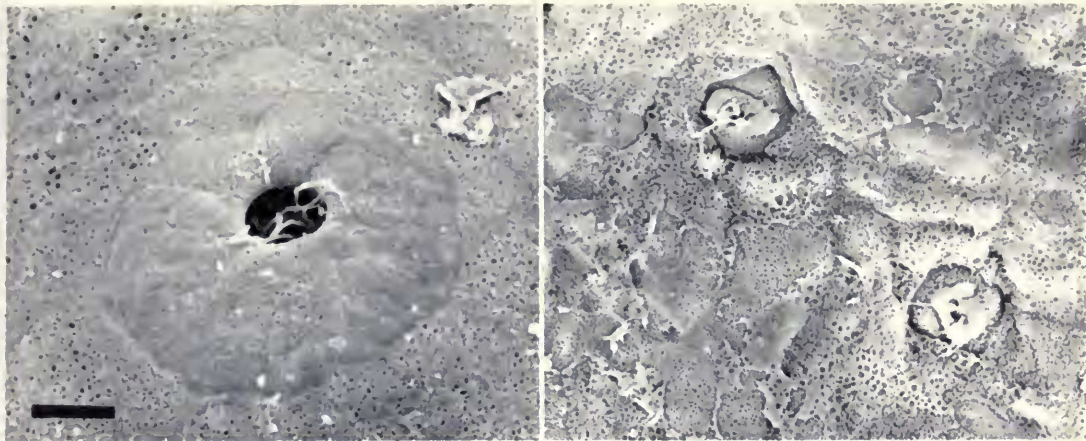
FIG. 14. Scanning electron micrograph close-up of neuromast organs in *Osteopilus brunneus* (**left**) and *O. septentrionalis* (**right**) larvae. Note that in *O. brunneus* neuromasts occur singly, whereas in *O. septentrionalis* neuromasts occur in groups of two. Scale line = 0.1 mm.

floor and roof papillae regress; and secretory rows in the branchial food traps disappear. The most remarkably "metamorphic" features of the pre-metamorphic *O. brunneus* tadpole are in the buccal pump and gut. The oblique orientation of the ceratohyals, enlarged hypobranchial plate, and reduced ceratohyals (reduced branchial baskets) collectively produce in *O. brunneus* a branchial skeleton virtually indistinguishable from that of a *Rana* tadpole at stage 43, i.e., in the middle of metamorphosis (cf. plate 22 in de Jongh, 1968). Similarly, the alimentary tract of our *O. brunneus* larva is like that of *Rana* and *Bufo* larvae in the middle of metamorphosis down to the level of minor folds and bends (cf. fig. 4 in Barrington, 1946).

Great attention has been given lately to how minor shifts in developmental timing produce major shifts in the phenotype of animals (Bonner, 1982). We feel that evolution of the *O. brunneus* larva from a more generalized hylid tadpole involved such a heterochronic process. Specifically we propose that most of the unique features of *O. brunneus* tadpoles evolved by an evolutionary shift in the onset signal of metamorphosis; α in the equations of Alberch et al. (1979). We suggest that many functional systems in the *O. brunneus* larva are actually beginning to metamorphose *before* they fully develop the typical larval pattern. However, the *rate* of metamorphosis has, if anything, been decreased, making the period of metamorphosis longer. *Osteopilus brunneus* does not complete metamorphosis early in an absolute sense. For most of their larval life, these tadpoles appear to arrest differentiation near the middle of meta-

morphosis. A similar shift in the timing of development has been proposed for the evolution of the arboreal, oophagous *Anotheca spinosa* larva (Wassersug, 1980). Such a shift may be the most common way in which obligatory macrophagous larvae have evolved. Evidently such shifts are evolutionarily simple, considering the multiple origins of arboreal macrophagy in tadpoles. Not all features, however, fit this evolutionary scenario, and morphological evolution in *O. brunneus* cannot be the result of a single shift in developmental timing. The most conspicuous feature of this tadpole, its elongate tail, is a specific larval specialization that is difficult to relate to premature onset of metamorphosis.
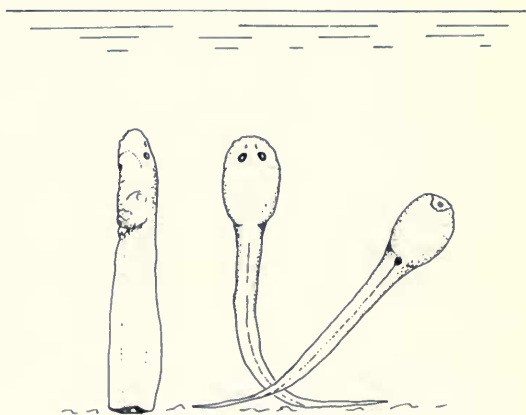

FIG. 15. Artist's depiction of *Osteopilus brunneus* larvae in their natural resting posture, based on laboratory observations.
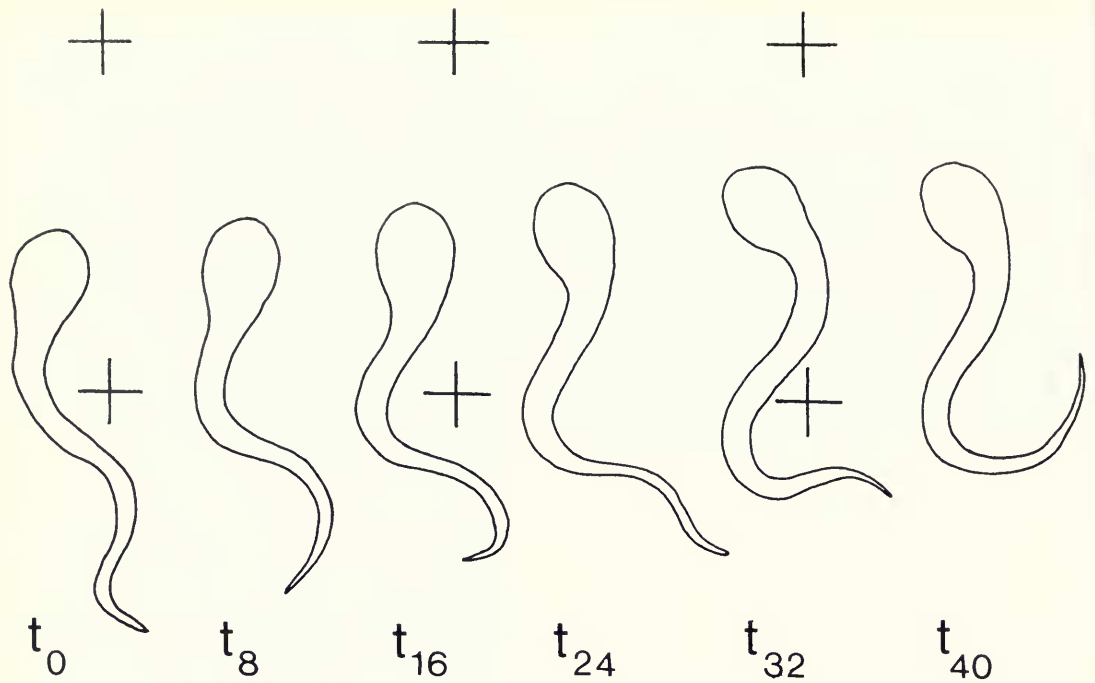
Fig. 16. Traces from a representative cine film of *Osteopilus brunneus* tadpole swimming at about 10 to 12 tail beats per second. The time between each frame in milliseconds is given below each figure. The distance between the crosses is 2 cm. Note the great amount of lateral movement at both the snout and tail tip.

Another morphological feature that does not fit this evolutionary scenario is the neuromasts of the lateral line system. At hatching, amphibian larvae usually have only one neuromast (termed the primary neuromast) present. With larval growth in many amphibians, primary neuromasts divide to form secondary neuromasts, which are oriented parallel to each other (Lannoo, 1985). These groups of secondary neuromasts are termed stitches (Harris & Milne, 1966). Unlike *O. septentrionalis,* the primary neuromasts of *O. brunneus* tadpoles do not divide to form secondary neuromasts and stitches. Because neuromasts and stitches simply degenerate at metamorphosis and are absorbed by the thickening skin, neuromast morphology in *O. brunneus* is typical of that in younger *O. septentrionalis.* Neuromast topography may, therefore, be considered relatively retarded in *O. brunneus.*

Larval Behavior

Tadpoles in rectangular and funnel-shaped containers under light and dark conditions were observed in the laboratory. Additional behavioral observations were made during the course of our experiments.

NORMAL RESTING POSTURE—Singularly or in groups, *Osteopilus brunneus* tadpoles in our laboratory were usually quiescent, even when exposed to extremely low DO concentrations and various food types. These tadpoles are negatively buoyant. They sometimes lay on the bottom of their tank, either on their belly or side. More commonly, they had an unusual posture in which their bodies were above the tank bottom with their snout pointed more or less upward, supported by the caudal portion of their elongate tail (fig. 15). The tail tip was on the substrate, bent laterally and curved either sharply or gradually into the long axis of the body as in the letter "J", depending on the angle of the body axis to the substrate (angle varied from 0° to 90°). This posture appears to require a bubble of air in either the mouth or lungs to make the rostral end of the tadpole buoyant; tadpoles denied access to air (see below) did not show this posture.

SWIMMING BEHAVIOR AND KINEMATICS—A variety of stimuli were used to elicit swimming behavior. Compared with either *Rana* or *Xenopus,* *Osteopilus* larvae responded weakly to mechanical or electrical stimuli but explosively to bright illumination, such as when floodlights were turned on for filming. In this situation the *Osteopilus* swam
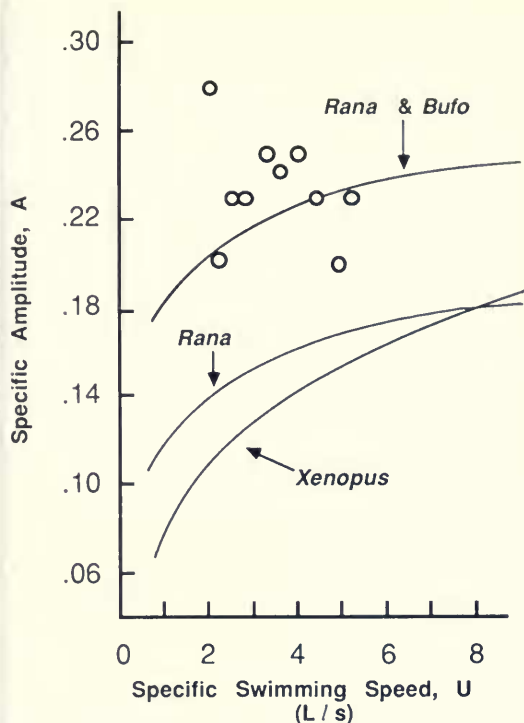
FIG. 17. Plot of maximum specific amplitude recorded at the tail tip against swimming speed. The circles represent data for *Osteopilus brunneus*. The three lines are significant log curve fits for comparable data from other species previously studied (Wassersug & Hoff, 1985; Hoff & Wassersug, 1986). The top line is for tadpoles with relatively short tails; i.e., *Rana catesbeiana* and *Bufo americanus*. The middle curve is for *Rana* larvae with proportionately longer tails: *R. septentrionalis* and *R. clamitans*. The lowest curve is for *Xenopus laevis* tadpoles. Note the relatively high maximum specific amplitude for *O. brunneus*. The relationship between these variables is not statistically significant for *O. brunneus*.

with their snouts in contact with the bottom and attempted to burrow into small depressions that were present near the corners of their tank. They rarely swam for any length of time in a straight line. In a flow tank, such as that used by Feder and Wassersug (1984), they showed little stamina.

Data were collected for 10 cine sequences of *O. brunneus* swimming at nearly constant velocity in a straight line over a range of speeds from 1 to 5 Ls^{-1}. Considering the variety of stimuli used in an effort to elicit maximum velocity, it is likely that 5 Ls^{-1} is near the maximum velocity that these larvae can attain. Traces from alternate frames of one representative sequence are shown in Figure 16. The time between each frame in this figure is 8 msec; the figure shows about one-half of a tail beat cycle.

As Figures 16 and 17 illustrate, swimming by *Osteopilus* larvae is characterized by a great deal of lateral movement compared to swimming in other tadpoles of comparable size (cf. figures in Wassersug & Hoff, 1985; Hoff & Wassersug, 1986). Maximum specific amplitude (at the tail tip) ranged from 0.20 to 0.28 L and was not correlated with swimming speed ($r = -0.28$, $P > 0.2$). Specific amplitude along the body varied from 0.09 L immediately behind the snout to 0.28 L at the tail tip. These values for lateral movement equal or exceed the highest values recorded for *Xenopus*, *Rana*, and *Bufo*.

The wave pattern in the tail of these tadpoles is not particularly uniform or stable. We found, for example, no correlation of wavelength with swimming speed ($r = -0.205$, $P > 0.5$).

Tail beat frequencies ranged from 3.8 to 23.0 s^{-1} and, as with other species, correlated positively
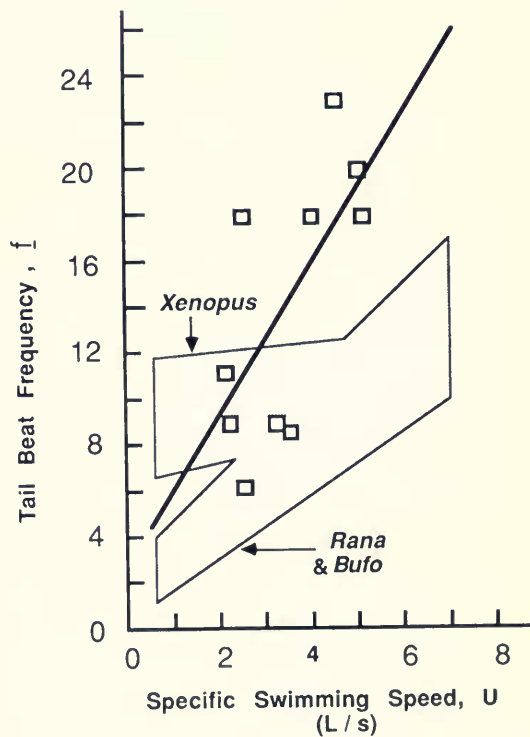

FIG. 18. Plot of tail beat frequency against specific swimming speed. Squares represent data for *Osteopilus brunneus*. The stippled area encompasses comparable data from previous studies of *Rana*, *Bufo*, and *Xenopus* (Wassersug & Hoff, 1985; Hoff & Wassersug, 1986). The regression line is only for *O. brunneus* and is $U = 2.51 + 3.36f$; $r = 0.67$, $P < 0.05$. Note the steep slope for the regression; at high speeds (>4 Ls^{-1}) *O. brunneus* larvae beat their tails approximately twice as fast as other tadpoles.
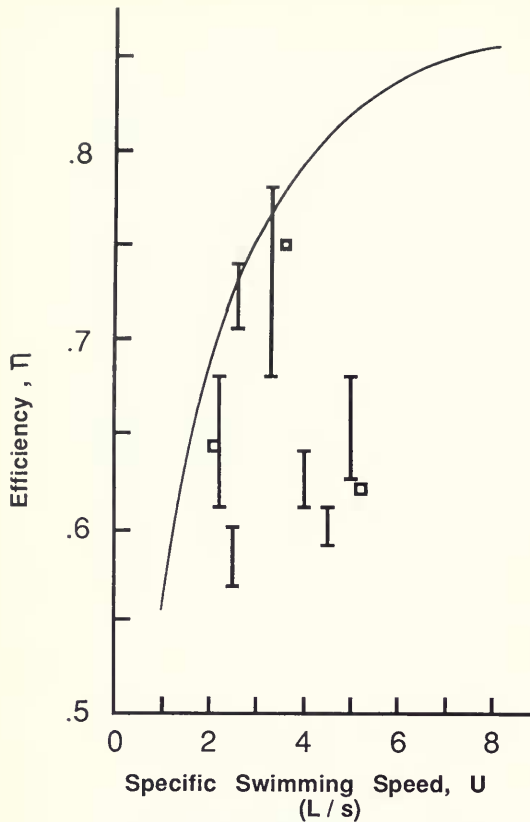
FIG. 19. Plot of the Froude efficiencies (η) of tadpoles against swimming speed, where η is one measure of kinematic or propeller efficiency (see text). Squares represent individual values for single swimming sequences of *Osteopilus brunneus* where variation in η was low. Vertical bars indicate ranges for efficiencies measured during single swimming bouts for *O. brunneus* where variation in η was high. The curve is a hyperbolic fit to comparable data for other species analyzed in Wassersug and Hoff (1985) and Hoff and Wassersug (1986). The η was significantly lower for *O. brunneus* than for the other species swimming in the same velocity range.

with swimming speed (fig. 18; $U = 2.51 + 3.36f$; $r = 0.66$, $P < 0.05$); but the slope of the *O. brunneus* line is much higher than that of other tadpoles swimming in the same speed range. Thus, when swimming at 5 Ls^{-1}, an *O. brunneus* tadpole must beat its tail nearly 20 s^{-1}, which is about twice as fast as a *Rana* or *Xenopus* larva needs to beat its tail to achieve the same velocity.

This difference is also reflected in the Froude efficiency (fig. 19), which is a derived measure of kinematic (propeller) efficiency [$\eta = 1 - 0.5 (1 - U/V)$, where V is the velocity of the propulsive wave traveling down the body]. For the swimming sequences we recorded, *O. brunneus* achieved the

same efficiency as that reported for *Rana, Bufo,* or *Xenopus* only twice. Froude efficiency did not correlate with swimming speed ($r = -0.21$; $P > 0.5$). Over the velocity range recorded here, Froude efficiency for *O. brunneus* averaged 0.60 (range 0.57–0.78), which was 20% below the average efficiencies for other larvae. This difference was significant (Mann-Whitney U test, $P = 0.05$).

Overall the kinematic data suggest that the *O. brunneus* larva is a light-shy, poor swimmer that (1) only swims sporadically; (2) can only achieve moderate velocities, even with very high tail beat frequencies; and (3) swims with excessive lateral motion indicative of low kinematic efficiency.

RESPIRATION PATTERNS—*Osteopilus brunneus* tadpoles do not buccal pump. There is no evidence of aquatic buccopharyngeal respiration of any sort. The tadpoles only opened their mouths to take in food or air.

There was an inverse correlation between DO levels and air gulping in *O. brunneus* in our experiment (fig. 20). An average rate of 18.4 air gulps/hour occurred at 1.5 mg/liter and became reduced to zero gulps in 30 minutes at 7.5 mg/liter. This relationship was not linear; a great decrease in air gulping occurred as DO concentration increased from 3.2 to 7.5 mg/liter (fig. 20).

Osteopilus brunneus tadpoles in nature probably never experience DO concentrations much higher than 5 mg/liter. The highest recorded by Laessle (1961) from *O. brunneus*-inhabited bromeliads was 2.3 mg/liter; Jones (1967) recorded a high of 2.7 mg/liter. At normoxic and saturated conditions in the laboratory, *O. brunneus* larvae show little or no aerial respiration. Because they neither pump water through their pharynx nor surface for air at high DO, their respiratory needs can be met at high DO solely by cutaneous respiration.

The highest aerial respiratory rates that we recorded for *O. brunneus* are, somewhat surprisingly, not atypical for tadpoles of other species at similarly low DO concentrations (Wassersug & Seibert, 1975; Feder, 1984; Feder & Wassersug, 1984; Wassersug & Feder, 1983; Marian et al., 1980). The linear regression given in Figure 20 has a relatively low slope. For other species, there appears to be a critical DO above which tadpoles avoid surfacing for air. If there is such a critical DO for *O. brunneus,* it occurs between 6 and 10 mg/liter. This is a high critical concentration compared with most tadpoles (values for other species range from 3 to 6 mg/liter in studies by Wassersug & Seibert, 1975; Feder, 1984; Marian et al., 1980; Feder & Wassersug, 1984) and above what *O.*
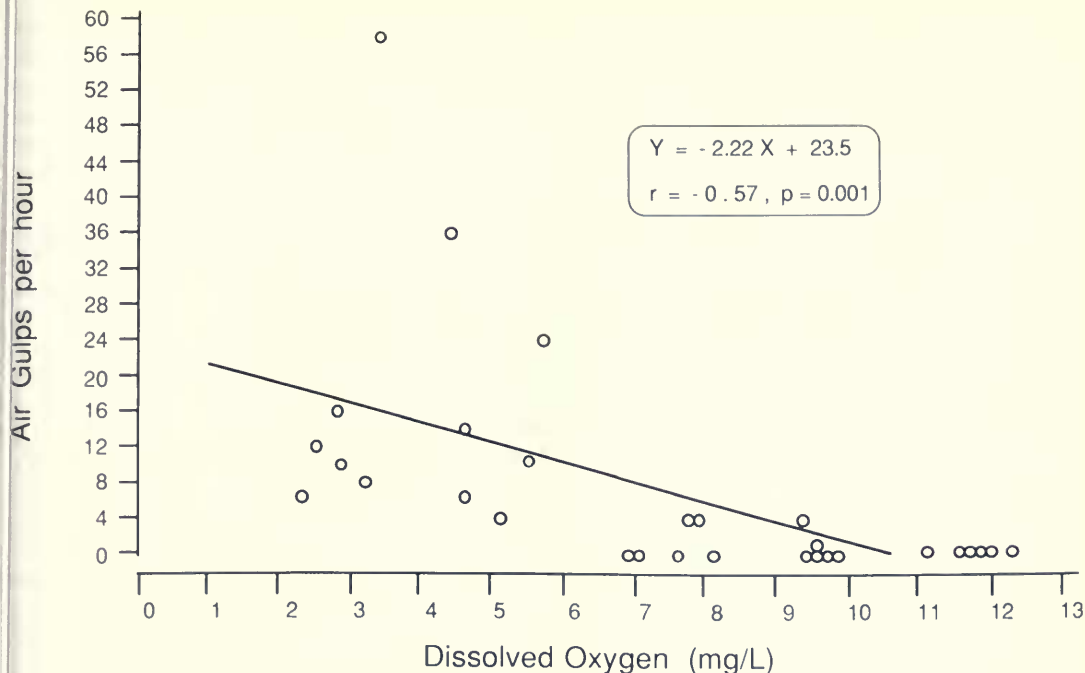
FIG. 20. Plot of the aerial respiratory frequency of *O. brunneus* larvae against dissolved oxygen in milligrams per liter. A linear regression was fitted to the data, with the regression equation and significance given on the figure.

brunneus larvae are likely to experience in nature. Thus, *O. brunneus* tadpoles at natural DO concentrations routinely breathe air, although they can survive for long periods through cutaneous respiration alone (see below). The shallow slope but high aerial respiratory frequency at moderate DO concentrations for *O. brunneus* characterizes tadpoles near metamorphosis in most other studies (e.g., Wassersug & Seibert, 1975) that have examined the ontogeny of aerial respiration in anuran larvae. Thus, the respiratory behavior is consistent with the argument given above (in the Larval Morphology section) that metamorphosis begins early in this species.

One other genus, *Hymenochirus*, has a tadpole known not to irrigate buccopharyngeal surfaces. Although these tadpoles are pond-dwelling, they are similar to *O. brunneus* in that they open their mouths only to take in air or live prey. They are strictly macrophagous and have even more reduction of larval branchial morphology than *O. brunneus*.

ANOXIC TOLERANCE—Only after artificially lowering DO concentrations, and at 1.7 mg/liter, did tadpoles begin to succumb to anoxia (fig. 21). All *Xenopus laevis* died after 120 minutes of exposure to hypoxic water with DO concentration reduced

to 1.7 mg/liter. All *Rana sylvatica* died after 150 minutes of hypoxia and at a DO concentration of 1.6 mg/liter. *Osteopilus brunneus* lasted another 90 minutes at this DO concentration, after a total of 240 minutes of extreme aquatic hypoxia. We then terminated the experiment. Four of these six *O. brunneus* tadpoles soon revived when placed
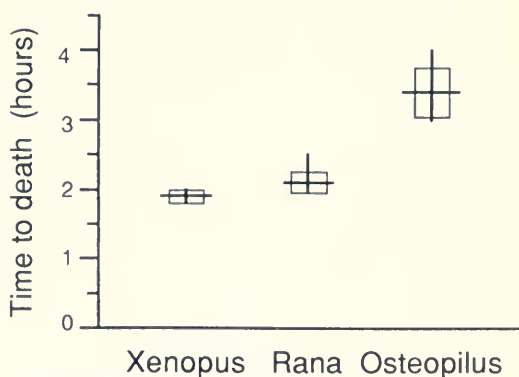

FIG. 21. The time to death for six tadpoles of each of three species exposed to extreme aquatic hypoxia and denied access to air. The crosses indicate means; the heavy vertical lines equal ranges; the height of the boxes equals two standard errors. Note the greater amount of anoxic tolerance for *Osteopilus brunneus* than for *Rana sylvatica* and *Xenopus laevis*.
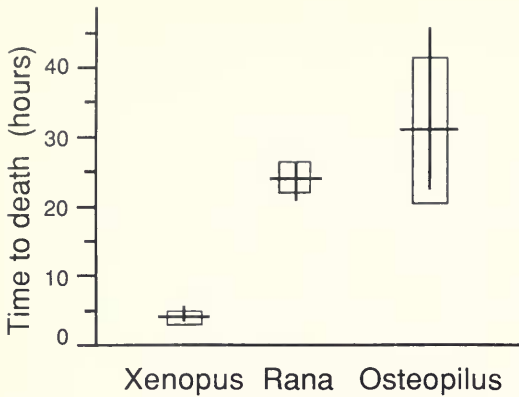
FIG. 22. The time to death for four tadpoles of each of three species on a wet substrate out of water. The crosses indicate means; heavy vertical lines equal ranges; height of the boxes equals two standard errors. Although the sample size is small, *Osteopilus brunneus* does exhibit greater absolute survivorship than *Rana sylvatica* or *Xenopus laevis*.

in oxygenated water. At the termination of the anoxic treatment, the DO concentration in the aerated control container was 11.1 mg/liter and all tadpoles were alive.

Both *Xenopus* and *Rana* tadpoles in the hypoxic tank initially swam continuously and frantically, then intermittently and less vigorously, toward the surface, prodding the screen with their snouts. *Osteopilus* remained quietly on the bottom for most of the time and only occasionally swam up toward the screen.

Although sample sizes are small, the difference in survival time between *O. brunneus* and the other species is striking. A lower activity level for *O. brunneus,* a higher anaerobic tolerance, or both, may account for the greater survivorship in this species.

RESISTANCE TO SUBAERIAL EXPOSURE—In this test *Xenopus* succumbed first, the last tadpole died after 5.5 hours ($\bar{x}$ = 4.0; fig. 22) of subaerial exposure. The *Rana* tadpoles lasted a maximum of 25.8 hours ($\bar{x}$ = 23.8; fig. 22). The first *Osteopilus* expired after 22.5 hours, the last after 46 hours ($\bar{x}$ = 31.1; fig. 22).

Early in the experiment, both *Xenopus* and *Rana* vigorously beat their tails when prodded, as if attempting to escape. However, *O. brunneus* beat their tails slowly one or two times. The greater survivorship for *O. brunneus* may reflect both their lower activity levels and the fact that they do not irrigate buccopharyngeal surfaces for respiration. Tadpoles that pump water through their gills, such as *Xenopus* and *Rana,* may suffocate as well as desiccate in subaerial conditions.

A similarly designed study was conducted by Valerio (1971) on Costa Rican tadpoles. Of six genera of tadpoles that he tested, only two species of *Leptodactylus* survived longer than our *Osteopilus*. Most species in the Costa Rican study had survivorships equal to or less than our *Rana*. *Leptodactylus* inhabit foam nests for part of their larval life. Valerio suggested that the high resistance of *Leptodactylus* related to their use of fast-drying ponds and independence from standing water. A similar argument may apply to *Osteopilus*; bromeliad tanks contain only small volumes of water, and prolonged dry periods occur even in rain forests. At our Hollywell field site, we experienced 14 consecutive days without rain during one of our visits.

Function of the Elongated Tail in *Osteopilus brunneus* Larvae

Elongation in arboreal tadpoles is primarily the result of tail lengthening and dorsal and ventral fin reduction; the *O. brunneus* larva with a tail to body ratio of 3.9 (table 3) is probably the most elongate tadpole known. Other extremely elongate tadpoles include the subaerial, semiterrestrial leptodactylid larvae *Cycloramphus* and *Thoropa*; their tail to body ratio, however, does not exceed 3.

Three functions have been proposed for the exceptionally long tail in *O. brunneus:* cutaneous respiration (Dunn, 1926); locomotion through a viscous medium (Noble, 1929; Jones, 1967); and agitation to aerate the water (Laessle, 1961). On the other hand, Dunn (1937) suggested that the short tail in *Anotheca spinosa* is an adaptation to confined spaces.

The cutaneous respiration argument, proposed by Dunn (1926) and others, of itself is not adequate to account for tail elongation in arboreal tadpoles. It suffers from a need to explain why the muscular portion of the tail is elongated while the tail fins, which in most tadpoles serve to increase tail surface area, are reduced. If the need for cutaneous respiration were the only selective force behind tail elongation in *O. brunneus,* one would expect well-developed tail fins, perhaps like those of *Hyla* in the *H. microcephala* species groups (see figures in Duellman, 1970). For *O. brunneus* and *O. septentrionalis* of the same total length (30 mm), *O. brunneus* has a tail surface area only 3% greater than that of *O. septentrionalis* (1.82 vs. 1.76 mm²). If we compare tadpoles of the same TL (17.5 mm), the surface area for *O. brunneus* (stage 25, total length 25 mm) is 47% *less* than that of *O. septentrionalis* (stage 31, total length 30 mm).

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Additionally, the fact that the gills are reduced in *O. brunneus* tadpoles is not consistent with a singular hypothesis of aquatic respiratory demand as the reason for tail elongation. Burggren and Mwalukoma (1983) have demonstrated a variety of morphological adaptations to chronic hypoxia in *Rana* that include proliferation of gill filaments and cutaneous capillary beds. *Osteopilus brunneus* larvae do not show any of these compensatory morphological responses to their naturally hypoxic environment.

At the low DO concentrations in which *O. brunneus* tadpoles are found, anuran larvae are more likely to shed oxygen to the water through their skin and buccopharyngeal surfaces than to absorb it (Feder & Burggren, 1984; Burggren & West, 1983). Thus, in complete contrast to Dunn (1926), we conclude that *O. brunneus* tadpoles have reduced their tail fin area to reduce aquatic gas exchange, rather than increase tail area to increase aquatic gas exchange. As an aside, Noble (1929) felt that gill loss in *O. brunneus* was somehow related to an "inhibitory effect of a dense medium on gill growth." In light of the fact that these tadpoles do not pump water through their mouths and may shed oxygen through gill surfaces to the water, this idea seems unlikely.

Noble (1929) and Jones (1967) suggested that tail elongation in *O. brunneus* is an adaptation to swimming in the viscous, egg capsule-water mixture of their bromeliad tanks. There is merit to this argument based upon kinematic considerations. Pond tadpoles, swimming in water, perform in the Reynolds numbers range of 5×10^2 to 5×10^4 (Wassersug & Heyer, 1983; see also fig. 16 in Wassersug & Hoff, 1985). If we replace, in the Reynolds number equation, the value for the kinematic viscosity of water with the lower value for glycerin—the liquid that Dunn (1926) and Jones (1967) felt was similar in viscosity to the fluid found in bromeliad tanks—the Reynolds number decreases to about 1 to 10, assuming tadpoles swim at the same speed. In fact, *O. brunneus* tadpoles swim about three times slower than *Rana* and *Xenopus*, reducing Reynolds number values even more. At these low Reynolds numbers, viscous forces predominate over inertial forces and may favor an elongate body (e.g., sperm, which swim with Reynolds numbers around 10^{-2}; Vogel, 1981).

Elongate bodies may be an adaptation for burrowing rather than swimming (Gans, 1975; Wassersug & Heyer, 1983). If a tadpole is adapted for swimming at higher Reynolds numbers, its body should be approximately streamlined. An object

TABLE 2. Fineness ratios for the majority of hylid tadpoles considered in this paper.

Species	Fine-ness ratio	Stage	Source
Osteopilus	9.7 (l)	37	Dunn, 1926
brunneus	7.2	27	This study
	7.3	37	This study
Osteopilus	3.4	27	This study
septentrionalis	3.5	37	This study
Calyptahyla	7.2	27	Dunn, 1926
crucialis			
Hyla wilderi	7.0	37	Dunn, 1926
Hyla marianae	8.4	37	Dunn, 1926
Anotheca	2.8 (d)*	27	Taylor, 1954
spinosa	4.8 (l)	27	Taylor, 1954
	5.2 (l)	35	Duellman, 1970
Hyla bromeliacia	8.1 (l)	37	Duellman, 1970
	6.2	36	This study
Hyla	6.9 (l)	37	Duellman, 1970
dendroscarta	4.4	25	This study
Hyla picadoi	4.4 (d)	31	Robertson, 1977
	5.3 (l)	31	Robertson, 1977
Hyla zetecki	6.1 (l)	37	Duellman, 1970

Fineness ratios = maximum body length : maximum body width. Values other than those measured by us were calculated from measurements taken from illustrations in the literature; (l) = drawings in lateral view, (d) = drawings in dorsal view. Tadpoles were staged according to Gosner (1960).
* Because all of these tadpoles tend to have more or less depressed bodies, maximum body width values based upon lateral views are lower than those based upon dorsal views, resulting in turn in higher fineness ratios. Not all authors provide dorsal views; where possible, we provide fineness ratios calculated from both views.

is considered most streamlined when it has a fineness ratio (maximum length/maximum diameter) of 4.5 (Alexander, 1968). Wassersug and Heyer (1983) have shown that several subaerial tadpoles (e.g., in the genera *Thoropa* and *Cycloramphus*) have fineness ratios greater than this (5.3 to 9.2). The fineness ratios of arboreal hylid tadpoles are given in Table 2 and indicate that tadpoles we categorize as elongate are too elongated to be strictly considered streamlined. However, the Reynolds number ranges over which most tadpoles swim (Wassersug & Hoff, 1985) are lower than that for which fineness ratios best predict minimum drag. The Froude efficiency of *O. brunneus* is so low compared with that of other tadpoles that it is hard to imagine how their exceptional elongation could be singularly adapted for efficient aquatic locomotion. Elongate arboreal tadpoles may instead

TABLE 3. Anuran species with free-living, arboreal larvae.

Family and species	Denticle pattern	Body form*	Tail/body ratio	Dietary information	Habitat information	References
HYLIDAE						
Hyla bromeliacia	2/4, 2/5	Attenuate	2.1	Plant matter, detritus, no evidence of oophagy	Bromeliads	Stuart, 1948; Duellman, 1970
Hyla dendroscarta	2/4	Attenuate	2.0	Plant matter, detritus, no evidence of oophagy	Bromeliads	Taylor, 1940; Duellman, 1970
Hyla picadoi	0/0, 1/1	Stout	1.7	Frog eggs only	Bromeliads	Robertson, 1977; Wassersug (pers. obs.)
Hyla zetecki	1/1	Stout	1.4	Frog eggs only	Bromeliads	Dunn, 1937; Duellman, 1970
Hyla marianae	0/0	Attenuate	2.9	Frog eggs (conspecific?)	Bromeliads	Dunn, 1926
Hyla wilderi	1/1	Attenuate	2.9	Frog eggs (conspecific?)	Bromeliads	Dunn, 1926
Anotheca spinosa	2/2	Stout	1.3	Frog eggs, insect matter	Bromeliads	Taylor, 1954; Duellman, 1970
Phrynohyas resinifictrix	2/3, 2/4	Typical pond tadpole proportions	1.6–1.9	Detritus	Tree holes	W. Pyburn (pers. comm.); B. Zimmerman (pers. comm.); R. McDiarmid (pers. comm.)
Osteocephalus [*buckleyi*]	...	...	...	...	Bromeliads, water at base of palm fronds	B. Zimmerman (pers. comm.)
Phyllodytes auratus	2/4, 2/5	Attenuate	1.7	...	Bromeliads	Kenny, 1969
Phyllodytes luteolus	2/4	Typical pond tadpole proportions	1.8	Detritus	Bromeliads	Bokermann, 1966; Peixoto (pers. comm.)
Phyllodytes tuberculosus	2/4	Typical pond tadpole proportions	1.8	Detritus	Bromeliads	Bokermann, 1966; Peixoto (pers. comm.)
Calyptahyla crucialis	1/0	Attenuate	2.9	Frog eggs (conspecific?)	Bromeliads	Dunn, 1926
Osteopilus brunneus	1/0	Very attenuate	3.9	Conspecific eggs	Bromeliads	Dunn, 1926; Orton, 1944; this paper
Ololygon perpusilla	2/3	Typical pond tadpole proportions	...	Detritus	*Neoregelia concentrica* and "other thorny edged bromeliads"	Lutz, 1973; Peixoto (pers. comm.)
LEPTODACTYLIDAE						
Crossodactylodes bokermanni or *izeckSoni*	2/3	Typical pond tadpole proportions	1.6	Detritus	Bromeliads	Peixoto, 1981; Peixoto, 1983 (pers. comm.)

TABLE 3. *Continued.*

Family and species	Denticle pattern	Body form*	Tail/body ratio	Dietary information	Habitat information	References
BUFONIDAE						
Mertensophryne micranotis	1/2	Attenuate	1.8	Macrophagy suspected	Tree holes, land snail shells	Grandison, 1980 (pers. comm.); Grandison & Ashe, 1983
RHACOPHORIDAE						
Theloderma stellatum	4/3	Stout	1.2	Irregular particulate matter, detritus	Tree holes	Wassersug et al., 1981
Theloderma horridum	4/3, 5/3	Stout	1.2	...	Tree holes	Boulenger, 1903; Wassersug et al., 1981
Philautus sp.	1/0	Attenuate	2.0	Frog eggs	Tree holes	Wassersug et al., 1981
Rhacophorus cf. *harrissoni*	4/3, 5/3	Typical pond tadpole proportions	1.6–2.1	Generalized diet	Tree holes	Wassersug et al., 1981; Inger (in press)
Nyctixalus pictus	5/3	Typical pond tadpole proportions	1.2	...	Tree holes	Wassersug et al., 1981
Nyctixalus spinosus	4/3, 5/3	Typical pond tadpole proportions	1.3–1.7	...	Tree holes	Taylor, 1962; Alcala & Brown, 1982
MICROHYLIDAE						
Ramanella triangularis	0/0	Stout	1.6–1.8	?	Tree holes	Inger et al, 1985
Hoplophryne rogersi	0/0	Attenuate	1.4	Plant (and animal) debris, conspecific egg fragments	Bamboo, banana leaves	Noble, 1929
Hoplophryne uluguruensis	0/0	Attenuate	1.7–2.0	Suspected to be the same as *H. rogersi*	Bamboo, banana leaves	Noble, 1929
Chaparina fusca	0/0	Typical microhylid proportions	1.7	...	Tree holes	Brown & Alcala, 1983; Parker, 1934; Inger, 1956
HYPEROLIIDAE						
Acanthixalus spinosus	4/3	Stout	1.4	Algae	Tree holes	Savage, 1952; Inger, 1966; Perret, 1962
RANIDAE						
Mantidactylus bicalcaratus	5/3, 6/3	Attenuate	?	...	Tree holes	Blommers-Schlösser, 1979; Razarihelisoa, 1974
DENDROBATIDAE						
Colostethus bromelicola	2/3	Typical pond tadpole proportions	1.5	Detritus	Bromeliads	Dixon & Rivero-Blanco, 1985; Dixon (pers. comm.)

TABLE 3. Continued.

Family and species	Denticle pattern	Body form*	Tail/body ratio	Dietary information	Habitat information	References
Dendrobates pumilio	0/1, 1/1	Typical pond tadpole proportions	1.7–2.2	Conspecific eggs	Bromeliads, terrestrial aroids	Weygoldt, 1980; Starrett, 1960
Dendrobates histrionicus (and *Dendrobates lehmanni*)	1/1	Typical pond tadpole proportions	1.5	Conspecific eggs	Bromeliads	Zimmermann & Zimmermann, 1985; Silverstone, 1975
Dendrobates arboreus	1/1	Typical pond tadpole proportions	2.2	...	Bromeliads?	Myers et al., 1984
Dendrobates speciosus	0/1	Typical pond tadpole proportions	2.0–2.1	Conspecific eggs	Bromeliads	Jungfer, 1985
Dendrobates auratus	2/3	Typical pond tadpole proportions	1.5	Protozoa, rotifers (omnivorous in laboratory)	Tree holes, bromeliads, stagnant pools	Silverstone, 1975; McDiarmid & Foster, 1975; Zimmermann, 1974
Dendrobates leucomelas	2/2	Typical pond tadpole proportions	1.8	Detritivore, possibly (but rarely) cannibalistic in laboratory	Tree holes, trunks, bromeliads	Zimmermann & Zimmermann, 1980; H. & E. Zimmermann (pers. comm.)
Dendrobates quinquevittatus (and *Dendrobates reticulatus*)	1/1 (1/1, 2/2)	Typical pond tadpole proportions	1.3	Omnivorous, cannibalistic, oophagous in captivity	Bromeliads	Zimmermann & Zimmermann, 1984
Phyllobates vittatus (and *Phyllobates lugubris*)	2/3	Typical pond tadpole proportions	1.5–1.7	Omnivorous in laboratory	Tree holes and bromeliads	Silverstone, 1976; Zimmermann, 1982; H. & E. Zimmermann (pers. comm.)

This is only a partial list of arboreal tadpoles. Excluded are a wealth of species that have free-swimming but nonfeeding arboreal larvae (e.g., the ranid *Phrynodon*; hylids *Flectonotus* and *Fritziana*; species in the microhylid genera *Kalophrynus*, *Platypelis*, *Plethodontohyla*, and *Anodontohyla*; and certain species of the bufonid genera *Pelophryne*, *Dendrophryniscus*, and *Frostius*). Other genera and species, such as the hylid *Nyctimantis rugiceps*, are regularly found calling from bamboo stumps and tree holes. Adults have even been found in association with large clutches of eggs, but the tadpoles have not been discovered. Additional species of *Ololygon* in the *O. perpusilla* group (Lutz & Lutz, 1939) are reported to have bromeliad tadpoles; however, their taxonomy is still under investigation (Peixoto, pers. comm.). Another microhylid is known to call exclusively from tree holes up to 6 m high, or possibly higher, off the ground (i.e., *Metaphrynella*, Inger, 1966; Dring, 1979), but the only larva described for this species (Berry, 1972) was collected in a swamp (see Wassersug et al., 1981). Based on the biology of the adults, one may expect to find further *Hyla*, *Mantidactylus*, and *Dendrobates* with arboreal larvae.

There is a semantic point about how close to the ground a tree hole needs to be to be an arboreal, rather than terrestrial, habitat. *Ololygon perpusilla* breeds in terrestrial bromeliads. A variety of ostensibly terrestrial, forest floor frogs (e.g., the microhylids *Hypopachus variolosus*, *Chaperina fusca*, and *Kalophrynus pleurostigma*) breed in very small, temporary bodies of water (McDiarmid & Foster, 1975; Inger, 1966), which can be in logs or at the base of trees where water collects between buttresses. The *Hypopachus variolosus* collected from such a situation by McDiarmid and Foster (1975) were in a hollow 87 cm above ground, containing approximately 10 liters of water.

* The information in this column refers to the shape of the head/body only, not the tail. As recognized by Orton (1953), all but the most generalized arboreal tadpoles have dorsoventrally depressed bodies.

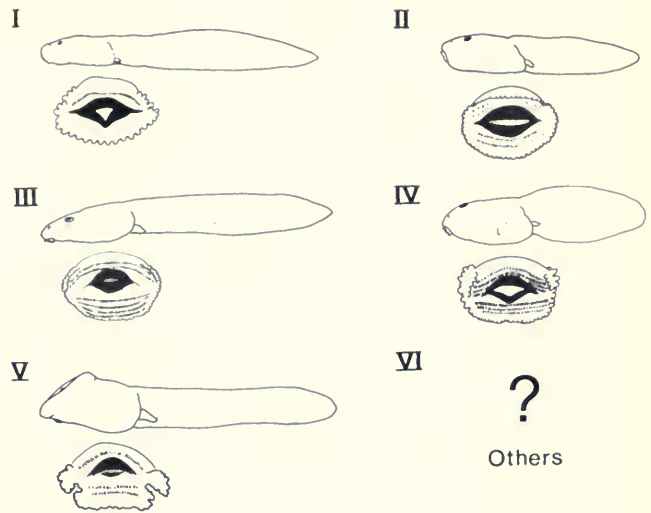FIG. 23. Schematic diagrams of representative tadpoles and their external mouth parts for the arboreal tadpole types recognized in this study. **I,** Elongate tadpoles with reduced denticle rows, represented by *Osteopilus brunneus* (Hylidae); **II,** shorter-tailed tadpoles with reduced denticle rows, represented by *Anotheca spinosa* (Hylidae); **III,** elongate tadpoles with increased denticle rows, represented by *Hyla bromeliacia* (Hylidae); **IV,** shorter-tailed tadpoles with increased denticle rows, represented by *Theloderma stellatum* (Rhacophoridae). **V,** *Mertensophryne micranotis* (Bufonidae), with its odd crown, is sufficiently strange to be considered a type by itself. **VI?,** Other distinctive types may also exist. Not included are the many arboreal tadpoles that do not feed. Only types I and II are either obligatorily (type I) or extensively (type II) oophagous.

be adapted for burrowing either into the detritus at the bottom or through the viscous fluid contained in the bromeliad tanks.

Last, we consider Laessle's (1961) proposal that the elongate tail of *O. brunneus* serves to agitate and aerate the water in bromeliad tanks. Laessle (1961, p. 515) asserted that *O. brunneus* tadpoles

> occupied the thin layer of jelly-free water at the surface, keeping their excessively long thin tails in constant agitation while not progressing appreciably. It appeared that their abdomens were stranded in the jelly and that most of the movement was imparted to the thin layer of water. In view of the low oxygen readings it seems that the function of the unusually long tail is to insure better aeration in the thin layer of water above the jelly.

These views, however, conflict with the behavior of undisturbed *O. brunneus* larvae in our laboratory. Laessle illustrated (his fig. 9) *O. brunneus* larvae oriented horizontally below the water surface in what he believed to be the natural posture of these tadpoles. In contrast (our fig. 15), we observe tadpoles most often vertical and quiescent. A similar head-up posture has been observed by Perret (1962) in *Acanthixalis spinosus* and in *Phrynohyas resinifictrix* by Pyburn (lab. obs.; pers. comm.). It was this motionless posture, with a resulting low-energy expense, that probably contributed to the relative success of *O. brunneus* in

our hypoxic and subaerial exposure experiments. The only time we observed vigorous swimming in tadpoles was when we disturbed them by turning on the 650-watt lights required for filming. We conclude that, in the process of trying to observe tadpoles in bromeliads (something we could not do without bending the leaves back and shining a flashlight into the central tank), Laessle disturbed them, and it was more likely that he observed the escape behavior of these tadpoles and not their normal posture.

In light of these three not completely satisfactory explanations for tail elongation in *O. brunneus* (respiration, aquatic locomotion, and aeration), we propose an additional view on the function of this long tail. We submit that the tail is a static postural organ, serving to position the body, and particularly the head of the tadpole, nearer to the water's surface. The lungs of these tadpoles serve as buoyancy organs and assist in this behavior. The advantage of this posture may reflect the importance of pulmonary ventilation to these animals by serving to reduce the energy involved in swimming to the surface (cf. Feder, 1984; Feder & Moran, 1985; Kramer, 1983). Or this posture may provide individuals with a competitive advantage by giving them the first opportunity to ingest eggs deposited by females at the surface.

Arboreal Tadpole Types

As part of this study, we have attempted to compare and contrast the morphology of a variety of

arboreal tadpoles, to better understand the links between the morphology and ecology of these organisms. Since Orton's (1953) study, several new arboreal tadpoles have been described, and her simple generalization of these animals as thin and flattened must be expanded. Table 3 summarizes most of what is known about arboreal larvae. It appears from this table at least five, possibly more, distinct types of arboreal tadpoles exist (fig. 23).

GROUP 1—Elongate tadpoles with attenuate bodies; tail/body ratios >2; denticle formula less than 2/3, usually reduced to 1/1 or less; highly reduced gill filters and gill filaments; musculoskeletal specializations for macrophagy or oophagy; little or no pigment. *Osteopilus brunneus* and the tadpoles of the other Jamaican hylids fit into this group. The arboreal *Hoplophryne, Philautus,* and some *Dendrobates* larvae also belong here.

These tadpoles are primarily associated with bromeliads and leaf axils rather than tree holes. They occur in relatively small volumes of water, which are likely to have little or no primary productivity as food for tadpoles. All the larvae in this group appear to be obligatorily oophagous during at least part of their lives. We suggest, as is known for several members of the *Dendrobates histrionicus* species group (e.g., *D. pumilio, D. speciosus,* and *D. histrionicus*), that all may depend on unfertilized, trophic eggs for food. Weygoldt (1987) has recently speculated on the evolution of tadpole attendance and oophagy in *Dendrobates*; unfortunately, not enough is known about other genera in this group to know if his ideas apply generally.

GROUP 2—Shorter tadpoles with stout bodies; tail/body ratios <2; denticle formula reduced to 2/2 or less; highly reduced gill filters and gill filaments; little or no pigment. Among the tadpoles that fit into this group are *Hyla zetecki, H. picadoi,* and *Anotheca spinosa.* These tadpoles are carnivorous and macrophagous. They are primarily associated with bromeliads which have relatively little free water. Conspecific frog eggs may form a major part of their diet, but the evidence for obligatory oophagy and trophic eggs is less well documented for this group than for the first group. The aggressive, omnivorous larvae of the *Dendrobates quinquevittatus* species group may belong here.

GROUP 3—Elongate tadpoles with attenuate bodies; tail/body ratio >1.7; denticle formula greater than 2/3; little or no reduction of the internal oral features associated with microphagous feeding in pond larvae (e.g., well-developed gill

filters); no specializations of the cranial musculoskeletal system for macrophagy.

In this group belong *Phyllodytes* species, *Hyla bromeliacia, H. dendroscarta,* and *Mantidactylus* species. There may be two different types of tadpoles here. First there are those, such as the hylids, that increase their denticle formula above the 2/3 common for pond larvae by adding one or two lower rows. The other subgroup appears to be made up of Old World forms that add two to four upper denticle rows, while retaining the traditional three lower rows.

Orton (1944) recognized the sharp distinction between the elongate arboreal tadpoles of group 1 and group 3, although she did not formally define the groups. Others (e.g., Salthe & Mecham, 1974, p. 445; Satel & Wassersug, 1981) have lumped the two types together, which has led to an unwarranted presumption about the trophic ecology of the group 3 larvae. It is clear from both morphology and stomach content analysis that group 3 tadpoles are neither normally oophagous nor particularly specialized for macrophagy. These tadpoles all appear to eat detritus found in their arboreal tanks. The literature suggests that they occur in very small bodies of water. Their elongated form appears to facilitate either insinuating themselves among leaf axils or subaerial locomotion between leaf axils, rather than swimming per se.

GROUP 4—Shorter tadpoles with stout bodies; tail/body ratios <2; denticle formula greater than 2/3 (typically with two to four extra rows superiorly); little or no reduction of internal oral features associated with macrophagy; gill filters and gill filaments normal to greater than normal density; darkly pigmented.

Tadpoles included in this group are rhacophorids in the genera *Rhacophorus, Theloderma,* and *Nyctixalus* as well as the hyperoliid *Acanthixalus.* This is primarily an Old World group, but not strictly so, since *Phrynohyas resinifictrix* evidently also belongs here. These larvae retain the internal oral morphology of tadpoles with generalized diets and aquatic, buccopharyngeal respiration. As such, they appear restricted to larger aquatic bodies, which are more likely to occur in tree holes than leaf axils.

GROUPS 5 AND 6 (OTHERS?)—The bufonid *Mertensophryne micranotis* is so different from other tadpoles that it may define its own group although it is most similar to tadpoles of group 1 (fig. 23). This tadpole lacks early lung development, and aerial respiration would seem limited for these

larvae. The strange crown on the head of this tadpole (and tadpoles of the related bufonid *Stephopaedes*; Channing, 1978), however, appears to keep the nostrils at or near the water's surface. This would allow for surface film respiration. Whether it also allows for aerial respiration via buccopharyngeal ventilation is not known.

A variety of tadpoles, which are not unusual for the families in which they occur (e.g., species in the microhylid genera *Microhyla, Chaperina, Kaloula conjuncta, Dendrobates auratus*; the leptodactylid *Crossodactylodes* spp., the dendrobatids *Colostethus bromelicola, Phyllobates vittatus* and *P. lugubris*, and hylids of the *Ololygon perpusilla* species group) are sometimes found in tree holes or leaf axils. Tadpoles like these may represent a morphological gradation between the generalized pond tadpole and more specialized arboreal tadpoles, such as those of group 2 above. Among *Dendrobates* there appears to be a complete spectrum from these generalized tadpoles (e.g., *D. auratus*) to aggressive, facultative carnivores (e.g., *D. quinquevittatus*) to obligate oophagous forms of the *histrionicus* species group.

Based on data reviewed here, we can make some predictions about the arboreal way of life for tadpoles.

1. Oophagy will be found, not in all arboreal tadpoles, but in ones with reduced numbers of denticle rows.
2. Tadpoles that are normally oophagous will feed on specialized, unfertilized, conspecific trophic eggs and not on fertilized eggs of either their own or other species.
3. Arboreal tadpoles with denticle formulas equal to or greater than 2/3 will be detritivores.
4. Detritivorous arboreal tadpoles with normal body proportions and relatively short tails will be restricted to the larger aerial containers, such as tree holes.
5. Extremely elongate arboreal tadpoles will occur in smaller aerial tanks, such as bromeliad leaf axils.
6. Arboreal tadpoles that normally live in hypoxic tanks will have morphological and behavioral specializations to reduce oxygen loss to the water and to augment either aerial respiration or surface film respiration. Such features may include: reduction of aquatic respiratory surfaces or reduced irrigation of such surfaces; low routine activity levels; vertical, head up swimming or resting posture; large, patent, anteriorly directed glottis.

Taxonomic Considerations

Throughout this paper we have accepted *O. brunneus* and *O. septentrionalis* as congeners (Trueb & Tyler, 1974) for the sake of morphological consideration. We conclude with a comment on the reasonableness of this taxonomic association.

In a classic paper on the concept of the genus, Inger (1958) argued that "each genus should represent the same kind of entity: a distinct mode of life and a distinct evolutionary shift." It is quite apt that Inger should have used tadpoles to illustrate his thesis. Following Inger's arguments, we consider it untenable that *O. brunneus* and *O. septentrionalis* be included in the same genus, despite the gross morphological similarities of their adults. The life histories of these frogs, particularly the morphology and ecology of their larvae, are too distinct—the evolutionary shift too great—for *Osteopilus* to be construed as a valid genus encompassing both species.

It may seem a simple matter to return one or the other species to the genus *Hyla*, since both have been there before (cf. Trueb & Tyler, 1974). However, this would not solve the problem, for Wassersug (1980), applying the same argument given above, has suggested that *Hyla* also does not form a single genus. Furthermore, we have not examined any specimens of the other species currently assigned to *Osteopilus, O. dominicensis*. The systematics of Carribean hylids is, in fact, currently under investigation by other workers using a variety of nonlarval characters (J. Bogart, R. Crombie, B. Hedges, pers. comm.).

Because the purpose of this study is not systematics, we resist making any formal taxonomic reassignments. We leave the matter open, but predict that further quantitative studies on the genetic similarities of the species will confirm that *brunneus* and *septentrionalis* should be in different genera.

Summary

We studied the morphology, ecology, and behavior of the arboreal tadpole of the Jamaican hylid, *Osteopilus brunneus*. Included in our morphological descriptions is information on the cranial myology, abdominal viscera, internal oral anatomy, chondrocranium, lateral line system, and overall growth. *Osteopilus brunneus* tadpole mor-

phology is compared to that of the currently recognized congener, *O. septentrionalis,* which has a generalized pond larva. The ecological and behavioral features that we examined in the laboratory included gut contents, normal resting posture, aerial respiratory behavior, swimming performance, ability to survive subaerial exposure, and tolerance to aquatic hypoxia. In the field the habitat and conspecific associations of adults, tadpoles, and eggs were recorded.

Our major results concerning *O. brunneus* larvae are as follows:

1. In the field larvae always co-occur with eggs—found either as gut contents or nearby—even when adults are not breeding.

2. Their major food item is undeveloped, conspecific eggs.

3. The stomach is a major storage organ that can hold more than 180 eggs in a large tadpole.

4. Larval growth is not isometric; most of the elongation of the tadpole is because of disproportionate tail elongation during early larval stages.

5. *Osteopilus brunneus* tadpoles are distinguished from *O. septentrionalis* by (*a*) wider buccal floor and mouth; (*b*) reduced buccal floor and roof papillae; (*c*) enlarged anteriorly directed glottis; (*d*) smaller and shallower branchial baskets with reduced gill filters; (*e*) reduced gill filaments; (*f*) no secretory ridges in the branchial food traps; (*g*) undivided dorsal velum; (*h*) enlarged orbitohyoideus and angularis musculature; (*i*) enlarged liver; (*j*) sacculate stomach; and (*k*) greatly reduced lateral line neuromasts.

6. The normal larval resting posture is with the snout pointing upward and the animal supported on the bottom by the terminal portion of the tail.

7. Larvae do not pump water through their buccopharyngeal cavity; they open their mouths only to take in air or food.

8. They are light-shy, poor swimmers that (*a*) swim sporadically; (*b*) can only achieve moderate velocities—ca. 5 body lengths per second; (*c*) swim with excessive lateral movement; and (*d*) have low kinematic efficiency.

9. They are obligate air-breathers at all levels of dissolved oxygen that they are likely to experience in the field.

10. They survive aquatic hypoxia and subaerial exposure longer than *Rana* and *Xenopus* tadpoles.

11. They have a reduced cutaneous surface area for their length, perhaps to prevent oxygen loss to the water across these surfaces.

12. Contrary to the conclusion of Laessle (1961),

the unusually elongate tail of these larvae is not used primarily to mix water nor is it specialized for aquatic respiration or aquatic locomotion.

Most of the unique morphological features of *O. brunneus* larvae can be accounted for by the evolution of an early metamorphic onset in an otherwise generalized larva. Metamorphosis itself is not accelerated, but the metamorphic process seems to begin before all typical features of pond larvae have fully developed. Not all morphological features of these larvae, however, can be explained by this evolutionary mechanism (e.g., lateral line neuromasts, tail elongation).

Oophagy in *O. brunneus* appears to involve specialized trophic eggs as has been reported in *Dendrobates pumilio, D. speciosus,* and *D. histrionicus.* This conclusion is based on the seasonality of fertilized egg production and undeveloped eggs ingested by larvae. Indirect evidence suggests that obligate oophagy in other arboreal tadpoles also involves specialized trophic eggs rather than simply cannibalism.

Based on what is known about the morphology and behavioral ecology of arboreal tadpoles in other families and genera, we expand Orton's (1953) classification for tadpoles to include five distinct arboreal tadpole types: (1) elongate tadpoles with denticle rows <2/3; (2) stout tadpoles with denticle rows <2/3; (3) elongate tadpoles with denticle rows >2/3; (4) stout tadpoles with denticle rows >2/3; and (5) *Mertensophryne micranotis.* Only types 1 and 2 are macrophagous or oophagous.

Following the ideas of Inger (1958) on the concept of the genus, we conclude that *Osteopilus brunneus* is not a valid congener of *O. septentrionalis.*

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